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A new genus and species of Ranidae (Amphibia, Anura) from south-western India

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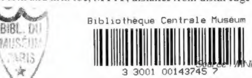
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A new genus and species of Ranidae is described from Karnataka and Kerala in south-western India. The new genus appears to belong in the subfamily Dicroglossinae. It shares with the genus *Fejervarya* Bolkay, 1915 the presence of fejervaryan lines on both sides of the belly, but differs from the latter genus in several respects, particularly in possessing a rictal gland at the mouth commissure and a white horizontal band along the upper lip, two characters that are common in the Indian Raninae but otherwise absent in the Dicroglossinae. It appears to be the fifth genus/subgenus of Ranidae endemic of southern India.

ABBREVIATIONS

Measurements. – EL, eye length (eye horizontal diameter); EN, distance from front of eye to nostril; FFTF, distance from maximum incurvation of web between fourth and fifth toe to tip of fourth toe; FL, femur length (from vent to knee); FLL, forelimb length (from elbow to base of outer palmar tubercle); FOL, foot length (from base of inner metatarsal tubercle to tip of fourth toe); FTL, length of fourth toe from basal border of proximal subarticular tubercle; HAL, hand length (from base of outer palmar tubercle to tip of third finger); HL, head length (from back of mandible to tip of snout); HW, head width; IBE, distance between back of eyes; IFE, distance between front of eyes; IMT, length of inner metatarsal tubercle; IN, internarial space; ITL, inner toe length; IUE, minimum distance between upper eyelids; MBE, distance from back of mandible to back of eye; MFE, distance from back of mandible to front of eye; MN, distance from back of mandible to nostril; MTFF, distance from distal edge of metatarsal tubercle to maximum incurvation of web between fourth and fifth toe; MTTF, distance from distal edge



of metatarsal tubercle to maximum incurvation of web between third and fourth toe; NS, distance from nostril to tip of snout; SL, distance from front of eye to tip of snout; SVL, snout-vent length; TFL, length of third finger from basal border of proximal subarticular tubercle; TFOL, length of tarsus and foot (from base of tarsus to tip of fourth toe); TFTF, distance from maximum incurvation of web between third and fourth toe to tip of fourth toe; TL, tibia length; TW, maximum "tibia" (actually shank) width; TYD, maximum tympanum diameter; TYE, tympanum-eye distance; UEW, maximum width of upper eyelid.

Museums, collections and persons. – AD, Alain Dubois; AMO, Annemarie Ohler; BMNH, Natural History Museum, London, United Kingdom; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MSNG, Museo Civico di Storia Naturale Giacomo Doria, Genova, Italy; MV, Michael Veith collection, Mainz, Germany; NMW, Naturhistorisches Museum, Wien, Austria; SDB, S. D. Biju; TBGRI, Tropical Botanic Garden and Research Institute, Thiruvananthapuram, Kerala, India; ZSI/SRS, Zoological Survey of India, Southern Regional Station, Madras, Tamil Nadu, India.

INTRODUCTION

Southern India, especially in its western part (Western Ghats or Sahyadris), is one of the richest biogeographic areas of the Oriental region. MYERS (1990) identified the Western Ghats as one among the 18 biodiversity hotspots of our planet. The amphibian fauna of this region is rich both in terms of species number and endemicity (INGER et al., 1987; BIJU, 2000). It also contains several endemic genera, in particular of the family Ranidae Rafinesque-Schmaltz, 1814 (sensu DUBOIS, 1992, i.e. including the Rhacophorinae Hoffman, 1932 as a subfamily) or epifamily Ranoidae (sensu VENCES & GLAW, 2001, i.e. including a family Ranidae and a family Rhacophoridae). In a traditional approach, supported by the latter proposal, the taxon Ranidae is understood as including only groups that lack intercalary elements between the penultimate and last phalanx of digits.

According to the highly provisional current working taxonomy of this family (see DUBOIS, 1999), the endemic ranid genera of the Western Ghat ranges include *Indirana* Laurent, 1986, *Micrixalus* Boulenger, 1888 and *Nyctibatrachus* Boulenger, 1882, three genera which belong in three different subfamilies. The genus *Indirana* is a member (and currently only genus: see BOSSUYT & MILINKOVICH, 2000, and VENCES et al., 2000*b*) of the Ranixalinae Dubois, 1987 (type-genus *Ranixalus* Dubois, 1986, a junior subjective synonym of *Indirana*: see DUBOIS, 1987*b*; subfamily sometimes incorrectly referred to as Indiraninae Blommers-Schlösser, 1993: see DUBOIS, 1999). The genus *Micrixalus* is the type-genus and only genus of the subfamily Micrixalinae (see BOSSUYT & MILINKOVICH, 2001); the nomen of the latter taxon, published without any diagnosis, is a nomen nudum (ANONYMOUS, 1999*a*); in tab. 1, we provide a diagnosis for this taxon. Finally, the genus *Nyctibatrachus* (synonym *Nannobatrachus* Boulenger, 1882; see DUBOIS, 1987*a*) is the type-genus and only genus of the subfamily Nyctibatrachinae Blommers-Schlösser, 1993 (see BLOMMERS-SCHLÖSSER, 1993; VENCES et al., 2000*b*).

In southern India, the nominative subfamily Raninae also occurs. It is represented there by a few species traditionally referred to the genus *Rana* Linnaeus, 1758, by some authors

(e.g., BOULENGER, 1920; DUTTA, 1997) to the subgenus *Hylarana* Tschudi, 1838 of this genus, and by DUBOIS (1992) to three provisional subgenera of this genus, two of which (*Hydrophylax* Fitzinger, 1843 and *Sylvirana* Dubois, 1992) also occur in other regions, but the third of which (*Clinotarsus* Mivart, 1869) is also an endemic of southern India.

We here report on the existence of a fifth group that also appears to be endemic of southern India, and that belongs to a fifth provisional subfamily of Ranidae, the Dicroglossinae Anderson, 1871. Before proceeding further, a few words are necessary concerning the tribal taxonomy of this subfamily. DUBOIS (1992) recognized four tribes in the latter: an African one with tadpoles (Conrauini Dubois, 1992), and three mostly Asian and Oriental ones, one with direct developing genera (Ceratobatrachini Boulenger, 1884), and two with tadpoles (Dicroglossini and Limnonectini Dubois, 1992). Recent data, especially molecular, lead to a re-evaluation of this taxonomy. First of all, MARMAYOU et al. (2000) showed that the genera *Occidozyga* Kuhl & Van Hasselt, 1822 and *Phrynoglossus* Peters, 1867 should be excluded from this subfamily, but the genus *Euphlyctis* Fitzinger, 1843, which is cladistically closely related to *Hoplobatrachus* Peters, 1863 and several other genera (BOSSUYT & MILINKOVITCH, 2000; VENCES et al., 2000*a-b*; KOSUCH et al., 2001) should be maintained in the Dicroglossinae; therefore the subfamily including the genera *Occidozyga* and *Phrynoglossus* should be called Occidozyginae Fei, Ye & Huang, 1991 (see DUBOIS, 1992). Secondly, a whole set of concordant data (BOSSUYT & MILINKOVITCH, 2000; EMERSON et al., 2000; MARMAYOU et al., 2000; VENCES et al., 2000*a-b*; KOSUCH et al., 2001; DELORME et al., submitted) suggest that at least three clades exist among Asian and Oriental Dicroglossinae. The first clade, for which the nomen Dicroglossini is available, includes the genera *Euphlyctis* Fitzinger, 1843, *Fejervarya* Bolkay, 1915, *Hoplobatrachus*, *Nannophrys* Günther, 1869 and *Sphaerotheca* Günther, 1859. The second clade includes one genus with tadpoles, *Limnonectes* Fitzinger, 1843, and one with direct development, *Taylorana* Dubois, 1987. MARMAYOU et al. (2000) showed that the origin of direct development was independent in the latter genus and in the genus *Philautus* Gistel, 1848 (Rhacophorinae/dae), but they did not study the cladistic relationships of the other direct developing genera placed by DUBOIS (1992) in the Ceratobatrachini. In a recent work, DELORME et al. (submitted) provided evidence that at least two of these genera (*Ceratobatrachus* Boulenger, 1884 and *Ingerana* Dubois, 1987) were not closely related to *Limnonectes* and *Taylorana*, nor to the other Dicroglossinae, and deserve recognition as an independent clade, for which the nomen Ceratobatrachinae is available. In the absence of additional evidence, we here transfer the genus *Taylorana* to the Limnonectini, but we maintain all other developing genera in the Ceratobatrachinae. This is however a provisional solution, until the cladistic position of all of them has been ascertained, as some of them might later prove to belong in fact in the Limnonectini. Finally, the data of DELORME et al. (submitted) also suggest that the group recognized by DUBOIS (1992) as a tribe Paini of the Raninae should be transferred to the Dicroglossinae, as a fourth tribe (including species that differ from those of all other tribes of this subfamily by their unforked omosternum). The subfamilial and tribal classification of the Ranidae will be discussed in more detail elsewhere (DUBOIS & OHLER, in preparation), but for the time being we just provide in tab. 1 some major diagnostic morphological characters for the five subfamilies mentioned above and for the two Asian tribes of Dicroglossinae with forked omosternum that include species with tadpoles (Dicroglossini and Limnonectini). The data summarized in this table will be useful to establish the place of the new taxon described below in the Ranidae.

Table 1. – Some diagnostic morphological characters of three subfamilies of the family Ranidae present in southern India. See GRANT et al. (1997) for a definition and discussion of the median lingual process. See DUBOIS (1995) for the definition of the tadpole's condensed collective keratodont formula (CCKF), i.e. minimum-maximum numbers of keratodont rows on upper/lower lips of tadpoles observed in the taxon. In "generic contents", genera present in southern India are marked with an asterisk.

Subfamily	Dicroglossinae Anderson, 1871	Dicroglossinae Anderson, 1871	Micrixalinae subfam. nov.
Tribe	Dicroglossini Anderson, 1871	Limnonectini Dubois, 1992	–
Type-genus	*Dicroglossus* Günther, 1860 (junior subjective synonym of *Euphlyctis* Fitzinger, 1843)	*Limnonectes* Fitzinger, 1843	*Micrixalus* Boulenger, 1888
Generic contents	*Euphlyctis** Fitzinger, 1843; *Fejervarya** Bolkay, 1915; *Hoplobatrachus** Peters, 1863; *Nannophrys* Günther, 1869; *Sphaerotheca** Günther, 1859	*Limnonectes* Fitzinger, 1843; *Taylorana* Dubois, 1987	*Micrixalus** Boulenger, 1888
Base of omosternum	Forked	Forked	Unforked
Vomerine teeth	Present	Present	Absent
Median ligual process	Absent	Absent	Present or absent
Digital disks	Absent	Absent or present	Present
Femoral glands	Absent or present	Absent	Absent
Vocal sacs in male	Present	Present or absent	Present
Nuptial pads in males	Present or absent	Absent	Present
Tadpole type	Aquatic or terrestrial	Aquatic or direct development	Aquatic
Tadpole's CCKF	1-5/2-6	1-3/2-3	1/0
References for characters	BOLKAY, 1915; DECKERT, 1938; LAURENT, 1950; KIRTISINGHE, 1958; CLARKE, 1981, 1983; DUBOIS, 1987*a*, 1992; FEI, 1999	DECKERT, 1938; LAURENT, 1986; DUBOIS, 1987*a*, 1992; FEI, 1999	BOULENGER, 1882, 1890; SMITH, 1924; DECKERT, 1938; MYERS, 1942*b*; INGER et al., 1984; DUBOIS, 1987*a*, 1992

Table 1. (continued)

Subfamily	Nyctibatrachinae Blommers-Schlösser, 1993	Raninae Rafinesque-Schmaltz, 1814	Ranixalinae Dubois, 1987
Tribe	–	Ranini Rafinesque-Schmaltz, 1814	–
Type-genus	*Nyctibatrachus* Boulenger, 1882	*Rana* Linnaeus, 1758	*Ranixalus* Dubois, 1986 (junior subjective synonym of *Indirana* Laurent, 1986)
Generic contents	*Nyctibatrachus** Boulenger, 1882	*Amolops* Cope, 1865; *Batrachylodes* Boulenger, 1887; *Nanorana* Günther, 1896; *Rana** Linnaeus, 1758; *Staurois* Cope, 1865	*Indirana** Laurent, 1986
Base of omosternum	Forked	Unforked	Forked
Vomerine teeth	Present	Present	Present
Median ligual process	Present	Absent	Present
Digital disks	Present	Absent or present	Present
Femoral glands	Present	Absent	Present
Vocal sacs in male	Absent	Present	Present or absent
Nuptial pads in males	Present	Present or absent	Present
Tadpole type	Aquatic	Aquatic	Terrestrial
Tadpole's CCKF	0/0	1-12/2-9	3-5/3-4
References for characters	BOULENGER, 1882, 1890; ANNANDALE, 1918, 1919; MYERS, 1942*a*; BHADURI & KRIPALANI, 1955; PILLAI, 1978; INGER et al., 1984; DUBOIS, 1987*a*, 1992; SHAFFER, 1988	DUBOIS, 1992	ANNANDALE, 1918; BOULENGER, 1920; RAO, 1920; INGER et al., 1984; LAURENT, 1986; DUBOIS, 1987*a*, 1992; SEKAR, 1992; BLOMMERS-SCHLÖSSER, 1993

MATERIAL AND METHODS

Specimens were collected in the field, fixed in 4 % formalin shortly after capture and stored in 70 % ethanol. The list of specimens examined and measured is given below under the description of the new species and in app. 1 for all other specimens, belonging to other species, used as comparative material.

Thirty-two measurements of adult and young specimens were taken by AMO with a slide calliper to the nearest 0.1 mm, or, for values below 5 mm, with an ocular micrometer to the nearest 0.01 mm. The list of measurements is given above under *Abbreviations*.

In order to facilitate comparisons, the description's methodology and plan were the same as those used in previous works on Asian anurans (Dubois & Ohler, 1998, 1999, 2000; Ohler & Dubois, 1999; Bossuyt & Dubois, 2001; Veith et al., 2001). The webbing formula is given according to Myers & Duellman (1982) and the tadpole keratodont formula according to Dubois (1995). A male specimen (MNHN 2000.3033) was partially dissected to ventrally examine the pectoral girdle. Drawings of an adult were made by AMO using a camera lucida (Wild Heerbrugg type 256576).

Morphometrical analyses and graphs were made using the SPSS statistical programs for personal computers (Norusis, 1992; Anonymous, 1999*b*). We used principal component analysis with varimax rotation (Anonymous, 1999*b*: 426) to show morphological distinctiveness of the new genus and canonical discriminant analysis to indicate morphological discrimination from *Fejervarya* and *Sphaerotheca*. One-way Tukey type b tests were performed on ranked ratios of all measurements between the six genera of Dicroglossinae. Detailed results of this analysis can be communicated upon request by the first authors, but are not given here because of space limitations.

Results and discussion

The data presented in detail below suggest that the new taxon discussed here is a new species that is the first known representative of a new genus of the Dicroglossinae Dicroglossini. We provide below a definition of the genus, followed by a comparison with other genera and a discussion of its relationships, and a detailed description of the species.

Minervarya gen. nov.

Type-species. – *Minervarya sahyadris* sp. nov.

Diagnosis. – Size small (SVL 17.6-19.2 mm in adult males, 20.6-23.0 mm in adult females); omosternum forked at base; vomerine teeth present; median lingual process absent; rictal gland present; digital extremities rounded, not dilated; webbing rudimentary; inner metatarsal tubercle very short and conical; external metatarsal tubercle present; tarsal ridge present; femoral glands absent; dorsal skin with longitudinal folds; lateral-line system absent in adult; fejervaryan lines present; upper lip with white horizontal band; nuptial pads present on prepollex and finger I of breeding male; vocal sac present, marked by glandular skin on middle of throat of adult male; aquatic tadpole with a keratodont formula of 2/3, keratodont rows simple; eggs of rather small size, white and brown colored.

Phenetic comparisons. – The combination of character states of the diagnosis above clearly excludes *Minervarya* from all subfamilies and tribes listed in tab. 1, except the tribe Dicroglossini of the Dicroglossinae. The tribes Conrauini and Paini can also be readily excluded,

the first one, among other characters, because of the keratodont formula of its tadpoles (CCKF 7-8/6-11; LAMOTTE & PERRET, 1968), and the second one, among other characters, by its unforked omosternum (DUBOIS, 1975, 1992). As a result of these comparisons, we propose to place the new genus in the tribe Dicroglossini. However, comparisons of the new species with the five genera referred here to this tribe point to the uniqueness of this species, that suggests that it belongs to a new, distinct genus.

The endemic Sri Lankan genus *Nannophrys* can readily be excluded from these comparisons, not only because of the very peculiar morphology of the adult, that has nothing to do with that of the new taxon (see e.g. KIRTISINGHE, 1957; CLARKE, 1983; DUTTA & MANAMENDRA-ARACHCHI, 1996), but also of its very peculiar tadpole (KIRTISINGHE, 1958). Remain four genera (tab. 1), all of which do occur in southern India, for which we provide detailed comparisons in tab. 2. For more security, in this table we also extended comparisons to the genus *Limnonectes*, that was placed by DUBOIS (1992) in the same tribe as *Fejervarya* and *Hoplobatrachus*, and to the three subgenera of *Rana* that are known to occur in southern India.

The data of tab. 2 show clearly that the new taxon does not fit by its combination of characters with any of the four other genera of Dicroglossini. Among them, of particular relevance is a comparison with the genus *Fejervarya*, with which it shares a rare character, the presence of fejervaryan lines (as defined by DUBOIS & OHLER, 2000: 35) on both sides of the belly (fig. 7). But the new taxon differs from the genus *Fejervarya* in several other important characters. In particular, the presence in this taxon of a rictal (mandibular) gland just posterior to the corner of the mouth (fig. 5) is unique in the subfamily Dicroglossinae, while this character is common in the subfamily Raninae (personal observations), including the Indian subgenera of *Rana* (fig. 6; tab. 2). Another important difference is the coloration of the upper lip of the adults (bright white) (fig. 5), that is not to be found in any other Dicroglossinae but is common in the Raninae, including the Indian subgenera of *Rana* (fig. 6; tab. 2). However, the forked omosternum of the new genus definitely excludes it from the Raninae as currently understood.

Minervarya differs from *Fejervarya* by the two characters mentioned above, and by its smaller adult size, the proportions of its head and hindlimbs, the aspect of its dorsal folds and of its vocal sacs. Beside the presence of fejervaryan lines and of rictal glands and the coloration of its upper lip, the new genus differs from all other Dicroglossinae, and in particular of Dicroglossini, by a number of characters (see tab. 1-2), among which only the most striking ones need to be mentioned here: from *Euphlyctis*, the new genus differs by its size, skin structure, webbing and tadpole's CCKF; from *Hoplobatrachus*, it differs by its size, webbing and tadpole's characters; from *Sphaerotheca*, it differs by its size, dorsal skin, shape of internal metatarsal tubercle and absence of femoral glands; from *Nannophrys*, it differs by its general shape and the whole morphology of tadpoles; finally, from *Limnonectes* (a genus member of the tribe Limnonectini of the Dicroglossinae), *Minervarya* differs by its size, undilated digital tips, webbing and presence of nuptial pads in adult breeding males.

Multivariate comparisons. – Morphometric data also confirm the uniqueness of this taxon. In several zoological groups, genera can be viewed as "shape groups", among which species are more similar in shape than with species of other genera (LEMEN & FREEMAN, 1984; DUBOIS, 1988*a-b*). This is particularly true in anuran amphibians, where morphometric differences

Table 2. – Some diagnostic morphological characters of nine genera or subgenera of the subfamilies Dicroglossinae and Raninae of the family Ranidae. See Ohler & Dubois (1989) for a definition of the different kinds of digital discs recognized here.

Genus	*Minervarya* gen. nov.	*Fejervarya* Bolkay, 1915	*Sphaerotheca* Günther, 1859
Adult male SVL	17-20	25-80	30-55
Adult female SVL	20-23	30-90	35-60
Head proportions (HW:HL)	Longer than wide	Longer than wide	Shorter than wide
Rictal gland	Present	Absent or present	Absent or present
Digit tips	Rounded	Pointed	Rounded
Webbing on feet	Rudimentary	Small to medium	Small
Internal metatarsal tubercle	Rather long, cylindrical	Long and narrow, cylindrical or shovel-shaped	Short, shovel-shaped
External metatarsal tubercle	Present	Absent or present	Absent
Tarsal ridge	Absent	Faint and short, or absent	Absent
Dorsal skin	With several longitudinal folds	With numerous longitudinal folds	Smooth
Upper lip coloration	With white horizontal band	With vertical brown bars	With vertical brown bars
Dorsal chevron	Absent	Present or absent	Absent
Shoulder spots	Absent	Present or absent	Present or absent
Tympanum coloration	Dark brown with its inferior border white	Dark spot on upper posterior part	Uniform or marbled, no distinct spot
Lateral line system in adult	Absent	Absent	Absent
Fejervaryan lines	Present	Present	Absent
Femoral glands	Absent	Absent	Present
Vocal sacs in male	Marked by darker coloration and skin differentiation on throat and chest	Marked by darker coloration, and sometimes also by longitudinal folds, on sides of throat	Marked by darker coloration and folds on sides of throat
Nuptial pads in male	Present on prepollex and finger I	Present on prepollex and finger I	Present on prepollex and finger I
Humeral glands in males	Absent	Absent	Absent
Tadpole's CCKF	2/3	2/3	2/3
Keratodont rows	Simple	Simple	Simple
References for characters	This paper	Boulenger, 1920; Dubois & Ohler, 2000; Veith et al., 2001	Boulenger, 1920; Kirtisinghe, 1958; Dutta & Manamendra-Arachchi, 1996

Table 2. (continued)

Genus	*Euphlyctis* Fitzinger, 1843	*Hoplobatrachus* Peters, 1863	*Limnonectes* Fitzinger, 1843
Adult male SVL	40-95	75-130	35-150
Adult female SVL	45-130	65-140	35-135
Head proportions (HW:HL)	As wide as long	As wide as long	As wide as long
Rictal gland	Absent	Absent	Absent
Digit tips	Pointed	Rounded	Rounded and dilated, sometimes with dorso-terminal grooves
Webbing on feet	Complete	Large	Medium to large
Internal metatarsal tubercle	Pointed, cylindrical, digit-like	Rather long, cylindrical or shovel-shaped	Rather long, cylindrical
External metatarsal tubercle	Absent	Absent	Absent
Tarsal ridge	Faint or absent	Long, distinct	Present, usually faint, or absent
Dorsal skin	Smooth with horny granules	With numerous longitudinal folds	Smooth or with longitudinal folds
Upper lip coloration	With or without vertical brown bars	With vertical brown bars	Without special coloration
Dorsal chevron	Absent	Absent	Present or absent
Shoulder spots	Absent	Absent	Absent
Tympanum coloration	Uniform, light	Uniform, light	Uniform or with an indistinct darker spot
Lateral line system in adult	Present	Absent	Absent
Fejervaryan lines	Absent	Absent	Absent
Femoral glands	Absent	Absent	Absent
Vocal sacs in male	Dark-coloured, projecting through two slits on sides of throat	Marked by colour and longitudinal folds on sides of throat	Present or absent
Nuptial pads in male	Absent	Present on prepollex and finger I	Absent
Humeral glands in males	Absent	Absent	Absent
Tadpole's CCKF	1/2	2-5/3-6	1-3/2-3
Keratodont rows	Simple	Double	Simple
References for characters	BOULENGER, 1920; KIRTISINGHE, 1958; DUTTA & MANAMENDRA-ARACHCHI, 1996	BOULENGER, 1920; DUBOIS, 1992; FEI, 1999; KOSUCH et al., 2001	BOULENGER, 1920; BOURRET, 1942; INGER, 1966, 1985; OHLER & DUBOIS, 1999

Table 2. (continued)

Genus	*Rana* Linnaeus, 1758	*Rana* Linnaeus, 1758	*Rana* Linnaeus, 1758
Subgenus	*Clinotarsus* Mivart, 1869	*Hydrophylax* Fitzinger, 1843	*Sylvirana* Dubois, 1992
Adult male SVL	42-55	59-65	34-80
Adult female SVL	63-85	40-70	30-83
Head proportions (HW.HL)	As wide as long or wider than long	As wide as long	As wide as long or longer than wide
Rictal gland	Absent	Present	Present
Digit tips	Rounded and dilated, sometimes with indistinct latero-ventral groove	Rounded and slightly dilated	Rounded and dilated, usually with latero-ventral groove
Webbing on feet	Large	Medium	Medium or large
Internal metatarsal tubercle	Rather long, oval, very prominent	Rather long, oval, very prominent	Rather short, oval or elliptic
External metatarsal tubercle	Absent	Present	Present
Tarsal ridge	Absent	Absent	Absent
Dorsal skin	Smooth, with dorso-lateral folds	Smooth or granular, with indistinct dorso-lateral folds	Smooth, with dorso-lateral folds
Upper lip coloration	With a blackish margin	With white horizontal band	With white horizontal band
Dorsal chevron	Absent	Absent	Absent
Shoulder spots	Absent	Absent	Absent
Tympanum coloration	Uniform, dark	Uniform, light-colored	Uniform, light colored
Lateral line system in adult	Absent	Absent	Absent
Fejervaryan lines	Absent	Absent	Absent
Femoral glands	Absent	Absent	Absent
Vocal sacs in male	Present	Present	Present
Nuptial pads in male	Present on prepollex and finger I	Present on prepollex and finger I	Present on prepollex and finger I
Humeral glands in males	Absent	Present	Present
Tadpole's CCKF	8/6-8	1/2-3	1-2/2-3
Keratodont rows	Simple	Simple	Simple
References for characters	Boulenger, 1920, Chari, 1962	Andersson, 1937; Chari, 1962	Boulenger, 1920; Kirtisinghe, 1957; Dubois, 1992, Dutta & Manamendra-Arachchi, 1996

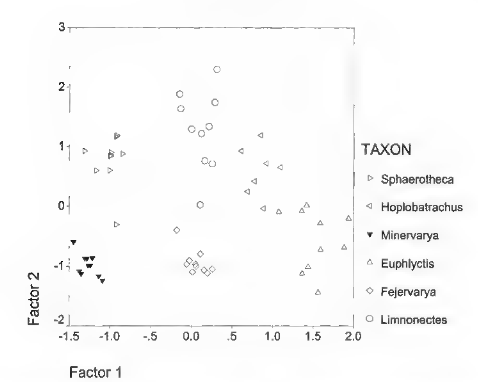


Fig. 1. Plots of factors 1 and 2 of principal component multivariate analysis based on varimax rotated coefficients from log-transposed characters (25 measurements) for the following genera: *Euphlyctis*, *Fejervarya*, *Hoplobatrachus*, *Limnonectes*, *Minervarya* and *Sphaerotheca*.

between species within genera are often very slight, if not absent, while differences between genera are often very clear-cut, thus allowing generic allocation of isolated species or individuals (HEYER, 1994; OHLER, 1996, DUBOIS & OHLER, 1999, VEITH et al., 2001), or recognition of new genera (DUBOIS, 1980; OHLER, 1999). The validity of this approach is once again confirmed in this study (tab. 3). As shown in fig. 1, the first and second factors of the principal component analysis based on 25 measurements sorted all genera of Dicroglossini, and also *Limnonectes*, as discrete groups. The new taxon appears as a new, discrete group, quite distinct from the other five groups, at least as distinct as they are between themselves. Morphologically it is closest to *Fejervarya* and *Sphaerotheca*. A discriminant analysis including these three genera (tab. 4, fig. 2) allowed to show that the measurements that best explain variation between groups are size, head shape, hind leg length and webbing.

One-way analysis including all six genera showed significant differences of the new genus in all but two measurements (HAL, TFL) to at least one of the other genera. The new taxon is the smallest species (SVL), it has the largest internarial distance (IN) and the shortest metatarsal tubercle (IMT). The new genus can be distinguished from *Fejervarya* by its wider head as expressed by IFE and IBE, its shorter head measurements (MFE, EN), larger eyes

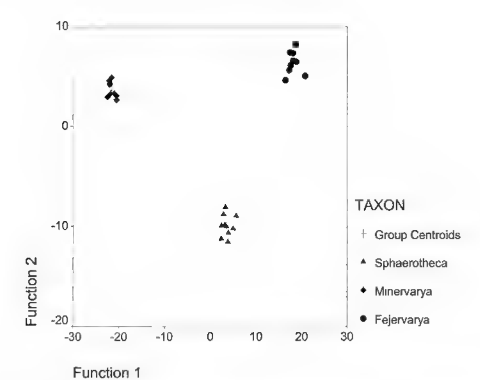


Fig. 2. Plots of canonical discriminant function scores using minimization of Wilk's lambda of morphometric log transposed characters (25 measurements) for the genera *Fejervarya*, *Minervarya* and *Sphaerotheca*.

(EL), shorter shank (TL), foot (FOL) and inner toe (ITL), and its reduced webbing (MTTF, MTFF). It can be differentiated from *Limnonectes* by its narrower (HW) and shorter (HL, MN, MBE, EN, TYE) head, its shorter forearm (FLL), shank (TL) and inner toe (ITL), but its longer fourth toe (FTL), and more reduced webbing (MTTF, MTFF, TFTF, FFTF). It differs from *Hoplobatrachus* by its head shape (MFE, IFE, IBE, TYE), its longer fourth toe (FTL), larger eyes (EL) and reduced webbing (MTTF, MTFF, TFTF, FFTF). It is distinguished from *Euphlyctis* by its wider head (IFE, IBE), larger eyes (EL) and reduced webbing (MTTF, MTFF, TFTF, FFTF). The morphological differences to *Sphaerotheca* are its narrower (HW, IFE) and longer head (MFE, MN, EN), longer shank (TL), foot (FOL) and fourth toe (FTL), and its reduced webbing (TFTF, FFTF).

Cladistic relationships. — As mentioned above, two important characters of the new taxon are not to be found in any known member of the Dicroglossinae but are common in the Raninae: (1) the presence of a rictal gland; (2) the coloration of the upper lip (bright white). However, these two characters are not unique to the Raninae, but can be observed in various other anuran taxa, where they probably appeared by convergence. On the other hand, the forked omosternum of the new species excludes it from the Raninae as currently understood. For the

Table 3. – Results of principal component analysis based on varimax rotated coefficients from log-transposed characters (25 measurements) for specimens referred to the genera *Euphlyctis*, *Fejervarya*, *Hoplobatrachus*, *Limnonectes*, *Minervarya* and *Sphaerotheca*.

	Initial Eigenvalues		
Component	Total	% of Variance	Cumulative %
1	22.639	90.558	90.558
2	0.799	3.196	93.754
3	0.696	2.783	96.537

	Rotation Sums of Squared Loadings		
Component	Total	% of Variance	Cumulative %
1	10.152	40.610	40.610
2	9.597	38.390	78.999
3	4.384	17.538	96.537

	Components for rotated component matrix		
Variable	1	2	3
SVL	0.649	0.621	0.422
HW	0.617	0.706	0.337
HL	0.673	0.647	0.340
MN	0.667	0.646	0.330
MFE	0.649	0.674	0.322
MBE	0.639	0.683	0.312
IFE	0.505	0.768	0.371
IBE	0.553	0.757	0.368
FLL	0.589	0.682	0.419
HAL	0.661	0.653	0.346
TL	0.732	0.530	0.410
FOL	0.709	0.534	0.456
IN	0.235	0.817	0.471
EN	0.698	0.592	0.353
EL	0.599	0.691	0.351
TYD	0.712	0.487	0.367
TYE	0.449	0.773	0.223
TFL	0.654	0.635	0.364
FTL	0.757	0.415	0.484
MTTF	0.836	0.453	0.299
TFTF	0.349	0.349	0.859
MTFF	0.830	0.463	0.297
FFTF	0.432	0.402	0.788
IMT	0.419	0.797	0.293
ITL	0.873	0.304	0.283

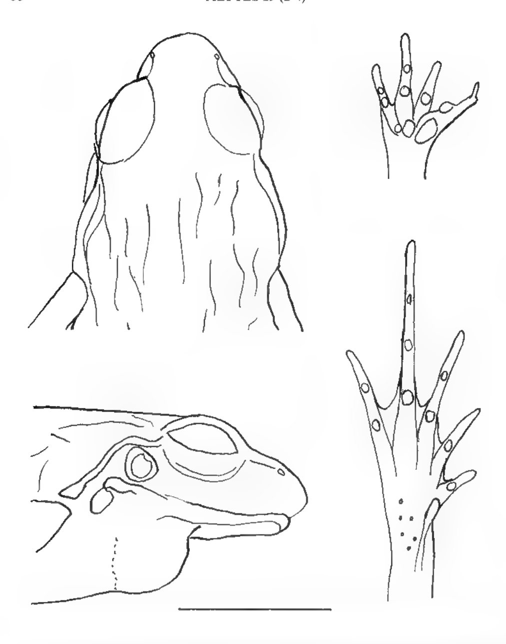


Fig. 3. – Holotype of *Minervarya sahyadris*, MNHN 2000.3031, adult male (SVL 19.1 mm). Top left, head from above; top right, right hand from below; bottom left, head from right side; bottom right, right foot from below.

Table 4. - Results of canonical discriminant analysis between specimens referred to the genera *Fejervarya*, *Minervarya* and *Sphaerotheca*.

A. Statistical significance

Eigenvalue	Canonical correlation	Wilks Lambda	Chi-square	Degrees of freedom	*P*
298.016	0.998	0.000	146.265	50	0.000
56.426	0.991	0.017	60.757	24	0.000

B. Standardized canonical discriminant function coefficients

Morphometric character	Function		Morphometric character	Function	
	1	2		1	2
SVL	- 5.472	- 0.465	FTL	- 0.092	- 3.222
HW	2.411	- 1.235	IN	- 6.213	2.296
HL	5.586	- 1.868	EN	0.992	0.957
MN	- 4.922	1.529	EL	3.284	- 2.374
MFE	1.366	2.573	TYD	3.701	- 2.020
MBE	- 0.320	- 2.749	TYE	2.179	- 0.410
IFE	- 0.381	- 1.919	MTTF	- 2.364	3.692
IBE	- 0.339	1.960	MTFF	4.273	2.344
FLL	- 1.372	- 0.188	TFTF	- 6.194	3.013
HAL	2.392	0.982	FFTF	2.974	1.112
TFL	- 1.859	- 0.410	IMT	- 3.768	- 0.743
TL	5.544	- 3.821	ITL	- 0.309	1.055
FOL	- 0.443	- 0.878			

C. Classification success

Actual group	Predicted group membership		
	Fejervarya	*Minervarya*	*Sphaerotheca*
Fejervarya	10 (100%)	0	0
Minervarya	0	10 (100%)	0
Sphaerotheca	0	0	10 (100%)

Table 5. - Some measurements and ratios of 6 adult males (the holotype* and 5 paratypes) of *Minervarya sahyadris* from the type-locality Gundia in Karnataka and two localities in Kerala (Mukkam, Thiruvanpady). SVL is given in mm, all other measurements are given as per thousands of SVL. Values given in the last two columns: mean ± standard deviation (range).

Collection number	MNHN 2000.3030	MNHN 2000.3031*	MNHN 2000.3033	TBGRI 2001.0006	TBGRI 2001.0007	MNHN 2000.3036	Total 3 adult males from Karnataka	Total 3 adult males from Kerala
Locality	Gundia	Gundia	Gundia	Mukkam	Mukkam	Thiruvanpady	Gundia	Mukkam + Thiruvanpady
SVL	18.9	19.1	18.0	17.2	18.5	19.0	18.7 ± 0.59 (18.0-19.1)	18.2 ±0.93 (17.2-19.0)
HW	344	319	317	366	341	358	327 ± 15.0 (317-344)	355 ± 13.1 (341-366)
HL	365	393	428	448	384	374	395 ±31.4 (365-428)	402 ± 40.1 (374-448)
MN	357	353	371	428	357	331	360 ± 6.6 (353-371)	372 ± 50.4 (331-428)
MFE	295	282	292	359	291	266	289 ±6.8 (282-295)	305 ± 48.2 (266-359)
MBE	178	153	173	206	172	147	168 ± 13.4 (153-178)	175 ± 29.9 (147-206)
IFE	199	170	180	211	196	194	183 ±14.9 (170-199)	200 ±9.2 (194-211)
IBE	285	258	267	302	281	293	270 ± 13.5 (258-285)	292 ± 10.7 (281-302)
FLL	209	186	205	234	217	225	200 ± 12.1 (186-209)	225 ± 8.2 (217-234)
HAL	223	207	194	237	238	232	208 ± 14.2 (194-223)	236 ± 3.3 (232-238)
TFL	96	119	112	132	133	140	109 ±11.8 (96-119)	135 ± 4.4 (132-140)
TL	434	424	428	459	465	458	429 ± 4.9 (424-434)	461 ± 3.7 (458-461)
FOL	534	456	483	494	486	537	491 ± 40.0 (456-534)	506 ± 27.1 (486-537)
FTL	336	298	263	316	301	331	299 ± 36.6 (263-336)	316 ± 15.0 (301-331)
IN	96	92	106	105	101	100	98 ± 7.2 (92-106)	102 ± 2.4 (100-105)
EN	76	68	92	78	74	75	78 ± 12.0 (68-92)	76 ± 2.0 (74-78)
EL	137	139	129	141	135	133	135 ± 5.1 (129-139)	136 ± 4.5 (133-141)
TYD	69	61	61	67	57	69	64 ± 4.6 (61-69)	64 ± 6.2 (57-69)
TYE	21	20	29	20	25	25	23 ± 5.1 (20-29)	23 ± 3.1 (20-25)
IMT	41	38	43	40	39	41	41 ± 2.9 (38-43)	40 ± 1.1 (39-41)
ITL	102	83	84	99	99	93	90 ± 10.6 (83-102)	97 ± 3.6 (93-99)
MTTF	202	173	177	188	186	187	184 ±15.8 (173-202)	187 ± 1.2 (186-188)
MTFF	202	176	180	188	189	191	186 ±13.9 (176-202)	190 ± 1.4 (188-191)
TFTF	305	302	263	302	291	331	290 ± 23.7 (263-305)	308 ± 20.8 (291-331)
FFTF	315	312	277	320	305	334	302 ± 21.1 (277-315)	320 ± 14.7 (305-334)

Table 6. – Some measurements and ratios of 4 adult female paratypes of *Minervarya sahyadris* from the type-locality Gundia in Karnataka. SVL is given in mm, all other measurements are given as per thousands of SVL. Values given in the last column: mean ± standard deviation (range)

Collection number	MNHN 2000.3027	MNHN 2000.3028	MNHN 2000.3029	MNHN 2000.3034	Total 4 adult females from Karnataka
SVL	22.3	23.0	21.9	20.6	22.0 ± 1.01 (20.6-23.0)
HW	327	326	329	316	324 ± 6.0 (316-329)
HL	345	352	370	384	363 ± 17.3 (345-384)
MN	302	313	352	346	328 ± 24.5 (302-352)
MFE	270	242	281	270	266 ± 16.7 (242-281)
MBE	169	147	157	167	160 ± 10.2 (147-169)
IFE	171	169	184	183	177 ± 7.5 (169-184)
IBE	273	253	263	270	265 ± 8.7 (253-273)
FLL	189	194	210	201	199 ± 9.2 (189-210)
HAL	212	217	219	201	212 ± 7.9 (201-219)
TFL	134	127	130	132	131 ± 2.9 (127-134)
TL	435	417	438	403	423 ± 16.5 (403-438)
FOL	507	474	511	456	487 ± 26.4 (456-511)
FTL	328	304	320	293	311 ± 15.8 (293-328)
IN	93	93	98	100	96 ± 3.4 (93-100)
EN	76	68	80	79	76 ± 5.4 (68-80)
EL	131	130	133	133	132 ± 1.8(130-133)
TYD	67	62	62	62	63 ± 2.3 (62-67)
TYE	17	25	26	19	22 ± 4.4 (17-26)
IMT	39	40	42	30	38 ± 5.5 (30-42)
ITL	100	100	100	94	98 ±3.2 (94-100)
MTTF	192	177	180	164	178 ± 11.6 (164-192)
MTFF	186	183	195	176	185 ± 8.0 (176-195)
TFTF	320	302	305	283	302 ± 15.1 (283-320)
FFTF	320	310	305	299	308 ± 8.8 (299-320)

time being, the cladistic significance of the state of the omosternum in the Ranidae (forked/unforked) is not yet clarified, especially as the recent data mentioned above in the *Introduction*, and especially those of DELORME et al. (submitted), suggest that a group of genera with unforked omosternum (the Paini) is cladistically nested within a clade of genera with forked omosternum (the Dicroglossinae), while other groups with forked omosternum (the Occydozyginae and Ceratobatrachinae) are apparently not part of the Dicroglossinae lineage. However, for the time being there exists no evidence of a genus with forked omosternum belonging in the well-identified clade to which the nomen Raninae applies.

Beside its forked omosternum, our main reason for referring the new genus to the tribe Dicroglossini is because it shares with the genus *Fejervarya* Bolkay, 1915 a unique character

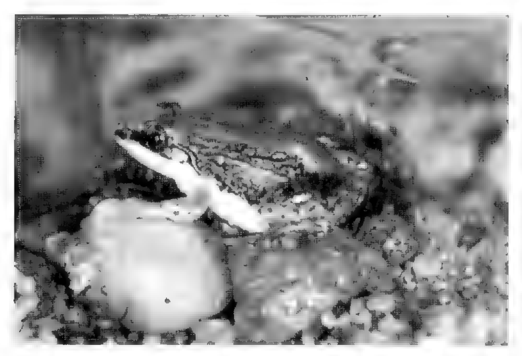


Fig. 4. A male specimen of *Minervarya sahyadris* (paratype, TBGRI 2001 0002) photographed in life on 24 August 1999 at Mukkam, Kozhikodu District, Kerala (photo S. D. Biju).

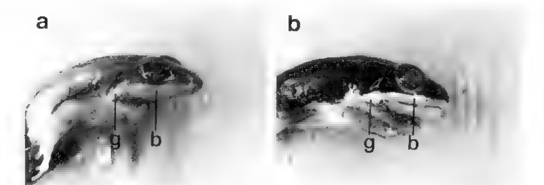
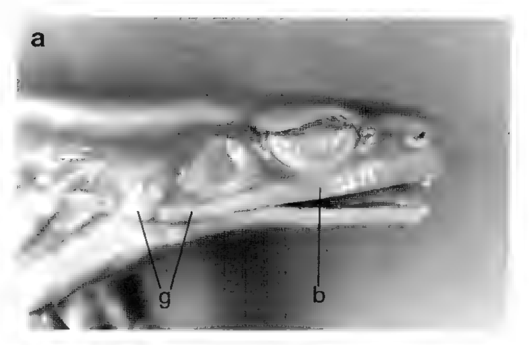


Fig. 5. Lateral view of head and body of *Minervarya sahyadris* (a) MNHN 2000 3031, adult male, holotype, Gundia, Karnataka, (b) TBGRI 2001 0007, adult male, Mukkam, Kerala. b, white band on upper lip, g, rectal gland.



b

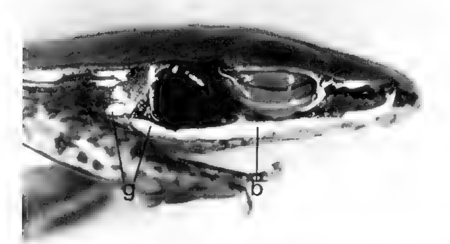


Fig. 6. Lateral view of head and body of (a) *Rana (Hydrophylax) malabarica*, MNHN 771, adult female, syntype, Malabar, India. (b) *Rana (Sylvirana) temporalis*, MNHN 2000 0613, adult male, Kitulgala, Sri Lanka. b, white band on upper lip; g, rictal gland.

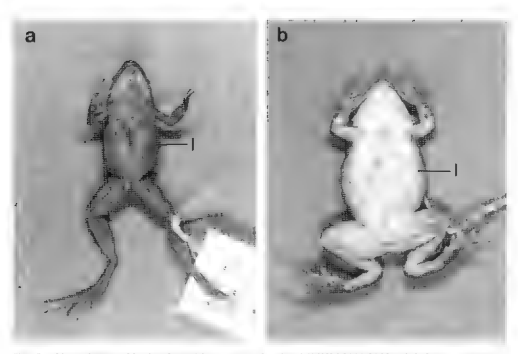


Fig. 7. Ventral view of body of (a) *Minervarya sahyadris*, MNHN 2000.3029, adult female, paratype, Gundia, Karnataka; (b) *Fejervarya limnocharis*, MNHN 1999.5723, adult female, Sapa, Vietnam. l, fejervaryan line.

among anurans, the presence on both sides of the belly of a fejervaryan line. We do not know of a single other genus of Anura showing this character. As both *Fejervarya* and *Minervarya* occur in southern India, we think it is more parsimonious to hypothesize a common origin of this character in these two genera than its independent occurrence by homoplasy. In the absence of contradictory information, we regard this character as a synapomorphy of both genera, that suggests that they are sister-genera. Molecular works are currently in progress to test this hypothesis.

Contents. For the time being, *Minervarya sahyadris* is the only known species of the genus *Minervarya*.

Distribution. The new genus is known from the states of Karnataka and Kerala in south-western India.

Vernacular name. We propose to use the name "minervarya" as vernacular name for these frogs, and "fejervarya" for frogs of the genus *Fejervarya*.

Etymology of the generic nomen. The generic nomen, derived from the Latin adjective *minimus*, "very small, the smallest", and from the zoological generic nomen *Fejervarya*, suggests that the new frog looks like a very small fejervarya. Furthermore, the new generic nomen includes the word *Minerva*, the Latin name of the Greek goddess of wisdom Athena, daughter of Zeus (Jupiter in Latin), who, according to her priests, leapt fully armed from the skull of her father: this evokes the behaviour of these tiny frogs, which suddenly jump, apparently from the mud or the ground, just like under the feet of a walking person.

Minervarya sahyadris sp. nov.

Holotype. - MNHN 2000 3031, adult male (SVL 19.1 mm), collected on 25 July 1984 by Alain Dubois along a rivulet in forest near the village of Gundia (13°05'N, 76°07'E; altitude about 200 m), Kempholey forest, Hassan District, Karnataka, India.

Paratopotypes. MNHN 2000.3026-3030, 2000.3032-3035, 5 adult males and 5 adult females, collected from 24 to 28 July 1984 by Alain Dubois at the same locality as the holotype.

Other paratypes. TBGRI 2001.0002-0007 and ZSI/SRS VA 1105, seven males, collected on 24 August 1999 by S. D. Biju at Mukkam (11°15'N, 75°43'E, altitude about 40 m), Kozhikodu District, Kerala, India; MNHN 2000.3036 and TBGRI 2001.0001, one adult male and one adult female, collected by S. D. Biju on 20 July 2001 in Thiruvanpady area (altitude about 30 m), about 30 km away from Kozhikodu, Kerala, India.

Description of holotype. MNHN 2000 3031, adult male (fig 3, 5), from Gundia (Karnataka, India)

(A) Size and general aspect. (1) Specimen of small size (SVL 19.1 mm), body moderately slender.

(B) Head. (2) Head of moderate size, longer (HL 6 1 mm) than wide (HW 7.5 mm, MN 6 74 mm; MFE 5.38 mm; MBE 2.92 mm), convex (3) Snout oval, protruding, its length (SL 3 05 mm) longer than horizontal diameter of eye (EL 2 66 mm). (4) Canthus rostralis rounded, loreal region concave, angle to upper surface of snout scarcely obtuse. (5) Interorbital space flat, larger (IUE 1 75 mm) than upper eyelid (UEW 1 62 mm) and as large as internarial distance (IN 1 75 mm); distance between front of eyes (IFE 3 24 mm) two third of distance between back of eyes (IBE 4.93 mm). (6) Nostrils rounded, with flap of skin laterally, closer to eye (EN 1 30 mm) than to tip of snout (NS 1.43 mm) (7) Pupil indistinct. (8) Tympanum (TYD 1 17 mm) distinct, rounded; about half of eye diameter, tympanum-eye distance (TYE 0.39 mm) one third its diameter. (9) Pineal ocellus absent (10) Vomerine ridge present, bearing few small teeth, between posterior parts of choanae, with an angle of 40° to body axis, closer to choanae than to each other, shorter than distance between them (11) Tongue moderate, oval, slightly emarginate; median lingual process absent (12) Supratympanic fold prominent, from eye to shoulder (13) Parotoid glands absent (14) Cephalic ridges absent. (15) Co-ossified skin absent

(C) Forelimbs. (16) Arm short, rather strong (FLL 3.56 mm), shorter than hand (HAL 3 95 mm), not enlarged. (17) Fingers rather long, thin (TFL 2 27 mm). (18) Relative length of fingers, shortest to longest: IV < II < I < III. (19) Tips of fingers bluntly rounded, not enlarged (20) Fingers without dermal fringe; webbing absent (21) Subarticular tubercles prominent, rounded, single, all present (22) Prepollex oval, prominent; two round, distinct palmar tubercles; supernumerary tubercles absent.

(D) Hindlimbs. – (23) Shanks three times longer (TL 8.1 mm) than wide (TW 2 92 mm), longer than thigh (FL 7 2 mm), but shorter than distance from base of internal metatarsal tubercle to tip of toe IV (FOL 8 7 mm) (24) Toes long, thin; toe IV long (FTL 5 70 mm) more

than one third of distance from base of tarsus to tip of toe IV (TFOL 13.5 mm). (25) Relative length of toes, shortest to longest: I < II < V < III < IV. (26) Tips of toes rounded, not enlarged (27) Webbing rudimentary: I 2 2 ½ II 2 3 1/3 III 3 4 IV 4 2 2/3 V (MTTF 3.31 mm, MTFF 3.37 mm; TFTF 5 77 mm; FFTF 5.96 mm). (28) Dermal fringe along toe V absent. (29) Subarticular tubercles prominent, oval, simple, all present (30) Inner metatarsal tubercle rather long, very prominent, spike-shaped; its length (IMT 0.72 mm) 2.22 times in length of toe I (ITL 1.59 mm). (31) Inner tarsal ridge present. (32) Outer metatarsal tubercle present, small, rounded, supernumerary tubercles absent; tarsal tubercle absent

(E) Skin – (33) Dorsal and lateral parts of head and body: snout, between the eyes and side of head smooth; back with indistinct, interrupted longitudinal glandular folds; upper part of flanks with glandular warts, lower part of flanks smooth. (34) Latero-dorsal folds absent (one of the dorsal folds in about the same position) (35) Dorsal parts of limbs: forelimbs smooth, thigh, shank and tarsus with indistinct glandular warts. (36) Ventral parts of head, body and limbs: throat and chest with dense glandular warts; belly smooth; thigh ventrally smooth, zone surrounding vent and posterior part of thigh with dense glandular warts. (37) Rictal gland present, just behind mouth commissure.

(F) Coloration in alcohol (38) Dorsal and lateral parts of head and body: dorsal parts of head and dorsum fawn colored, with indistinct mid-dorsal line and lighter longitudinal bands; a large light beige band from posterior border of eye to groin, underlined ventrally by a brown band, loreal region, tympanic region, supratympanic fold and tympanum brown; upper lip with a whitish horizontal band, rictal gland white. (39) Dorsal parts of limbs: forelimbs, thigh, shank and foot beige with brown bands; posterior part of thigh light brown. (40) Ventral parts of head, body and limbs. throat light grey; margin of throat yellowish without spots or bands; chest, belly and thigh yellowish. Vocal sac light grey in its anterior part and yellowish in its posterior part (including throat and chest).

(G) Male secondary sexual characters. - (41) Nuptial spines present, one single patch on prepollex and finger I up to half penultimate phallange numerous, very small, whitish spines. (42) Vocal sac present, unique subgular pouch, marked by glandular skin on middle of throat and anterior chest; a pair of rounded openings in rather posterior part of mouth floor. (43) No other male secondary characters.

Variation - Measurements of minervarya specimens are given in tab. 5-6 Due to the small number of specimens no statistical analysis has been performed All 6 adult males measured are smaller (SVL 17.2-19.1 mm) than the 4 adult females (SVL 20 6 23.0 mm), a sex size dimorphism which, although not testable statistically (DUBOIS, 1984), is probably significant and general in the species. Individuals of different origin seem very similar in their measurements, except concerning the limbs: the forelimb (FLL), hand (HAL), third finger (TFL) and tibia (TL) appear shorter in the specimens of both sexes from Karnataka than in the males from Kerala; at least the two series of measurements do not overlap in range Such a trend would need to be confirmed on much larger series of specimens. In the specimens from Gundia in life, when the hind leg was extended anteriorly along flank, the heel reached a point situated from back of tympanum to slightly beyond back of eye. The series from Kerala is much clearer in coloration, but shows no differentiation in color pattern This variation may be due to storage and age of the specimens. The males from Kerala have a greyish pattern on the throat which

reminds the gular "W" of fejervarya males. In the minervarya specimens from Karnataka, the greyish zone is much more indistinct. All males have a glandular skin under the vocal sac which extends to the anterior part of the chest. The rictal gland can be observed on all specimens.

Colours in life (fig. 4). – Iris clear golden in its upper part, darker in its lower part. Pupilla horizontal oval, continued anteriorly and posteriorly in iris by a dark horizontal bar, and inferiorly by a narrow dark vertical line. Sides of head dark brown, darker in tympanic region. Upper lip with a bright white bar, from snout to below tympanum or posteriorly, particularly bright in its anterior part. Mid dorsum brick red, reddish, reddish brown, brown, greyish or golden, often with a creamish, golden, yellowish or reddish mid-dorsal line or band (indistinct after fixation). Indistinct, discontinuous colored bands on sides of back, especially in its posterior part, in the usual place of latero-dorsal folds in frogs, but supported by folds that are not different from or more prominent than the other longitudinal folds of back. Upper flanks dark greyish with indistinct clearer zones, lower flanks darker. Upper arm brick red or brown. A clear median line sometimes present on upper part of hind leg from vent to heel. Throat translucent or yellowish in its anterior part, followed by a greyish zone, and by a yellow posterior part. Chest and belly bright white, yellow or yellowish. Translucent fejervaryan lines quite distinct. Inferior part of thighs translucent or clear yellowish.

Natural history. – In Karnataka the species was collected in open habitat in forested area (Kempholey forest), in Kerala it was found near paddy fields and in an abandoned quarry. During monsoon (June-July), the males call from terrestrial calling sites, never in water, but always turned towards water (small ponds or rivulets). Calls are rapid sequences of high-pitched "*chick*... *chick*...", reminding the jingling of a bunch of keys. Amplexus is axillary. Eggs masses are attached to aquatic vegetation. They are composed of 20-35 eggs that are 2 mm in diameter and pigmented. Tadpoles (that will be described in detail elsewhere) are typical ranid tadpoles, with unspecialized, ventrally directed mouthparts and a keratodont formula of 1:1+1/1+1:2. In captive condition they were observed to reach metamorphosis within 28 days.

Etymology of the specific nomen. – The specific nomen is the Sanskrit name *Sahyadris*, meaning "the mountains" (*adri*) "of the Western Ghats" (*Sahyan*): it refers to the area of distribution of the species.

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APPENDIX 1

COMPARATIVE MATERIAL EXAMINED

Specimens marked with an asterisk (*) were included in the morphometric analyses (tab. 3-4, fig. 1-2).

Conraua alleni (Barbour & Loveridge, 1927). – SIERRA LEONE: *Region of Loma*: MNHN 1979.6136-6146.

Conraua beccarii (Boulenger, 1911). – ETHIOPIA: *Gondar*, 2000 m: MNHN 1933.0021.

Conraua crassipes (Buchholz & Peters, 1875). – NIGERIA: *Idanre*: MNHN 1995.5704-5708, 1995.5711, 1995.5715.

Conraua derooi Hulselmans, 1972. – TOGO: *Dangi Angba*: MNHN 1978.2026-2031; *Misahohe*: MNHN 1993.4084-4087.

Conraua goliath (Boulenger, 1906) – EQUATORIAL GUINEA: MNHN 1992.5316

Euphlyctis cyanophlyctis (Schneider, 1799). NEPAL *Dillikot*, 2400 m MNHN 1975 2164*, 1975 2182*-2183*, 1975 2194*, 1975.2196*, *Samchare* MNHN 1977 1364-1403, *Surkhet*, 900 m MNHN 1996 9274-9280, *Tatopani Khola*, 2200 m: MNHN 1975.2250-2273

Euphlyctis hexadactylus (Lesson, 1834). – INDIA: NMW 2512.1*-5*, 25121*.

Fejervarya greenii (Boulenger, 1904) SRI LANKA *Nuwara Eliya* MNHN 2000.0617

Fejervarya keralensis (Dubois, 1981) INDIA. *Coonoor Nilgiris* MNHN 1902 0124-0127, *Genji, Coromandel*: MNHN 1902.0172.

Fejervarya limnocharis (Gravenhorst, 1829) – INDONESIA: *Java, Bogor* FMNH 256721*-256724*, *Java, Chianjur*, FMNH 256727*-256728*, 256732*, *Sumatra, Medan*. FMNH 256758*; *Sumatra, Seleukat* FMNH 256769* , *Sumatra, Sidikalang* FMNH 256762* LAOS *Luang Prabang* MNHN 1999 6093 THAILAND: *Khao Chong, Trang* MNHN 1987 2357-2385. VIETNAM *Sapa* . MNHN 1996.3373 3376

Fejervarya nepalensis (Dubois, 1975) NEPAL *Godavari* MNHN 1975 1607-1624, *Joubari* MNHN 1975 1640-1645.

Fejervarya nilagirica (Jerdon, 1853) · INDIA *Udhagamangalam, Nilgiris* MNHN 1984 2334-2342

Fejervarya pierrei (Dubois, 1975). – NEPAL: *Birtamode*. MNHN 1975 1681-1710

Fejervarya rufescens (Jerdon, 1853) · INDIA *Gundia, Karnataka* MNHN 1984.2349-2355.

Fejervarya syhadrensis (Annandale, 1919) NEPAL *Dongison* MNHN 1975 2038-2062, *Tir Pani Khola* MNHN 1996.9259-9265.

Fejervarya teraiensis (Dubois, 1984). – NEPAL: *Birtamode*. MNHN 1976 1029-1040

Fejervarya vittigera (Wiegmann, 1834) · PHILIPPINES *Manilla* MNHN 1900 0435-0437, 1994.0568.

Hoplobatrachus chinensis (Osbeck, 1765) [valid nomen of the species often referred to as *Rana rugulosa* Wiegmann, 1834. see KOSUCH et al., 2001, and DUBOIS & OHLER, in preparation]. –CHINA "*Canton*": BMNH 1933 12.4 18*, *Cap Syngmore* ZMB 3271* , *Hong Kong*: NMW 2614 5* · LAOS *Vientiane, market*: MNHN 1997.4900*. – MYANMAR: *Pegu*: BMNH 1868.4.3.90*.

Hoplobatrachus crassus (Jerdon, 1853). – INDIA: *Madras* BMNH 1872 4.17.245*.

Hoplobatrachus occipitalis (Gunther, 1859). GAMBIA BMNH 1947 2 29 8* IVORY COAST *Soubré* MNHN 1990 4428, *Soubré Sanandra* MNHN 1993 2845 ; *Tabou*. MNHN 1990 4386-4389. LIBERIA *Nimba, Grassfield* MNHN 1990 4380-4385

Indirana brachytarsus (Gunther, 1876) INDIA *Ponmudi, Trivandrum District, Kerala* FMNH 217954

Indirana diplosticta (Gunther, 1876). – INDIA: *Malabar*. BMNH 1947 2.3.27

Limnonectes kuhlii (Tschudi, 1838) INDONESIA *Sumatra Sidikalang* MV 80*, MV 82*, MV 102* 103*, MV 105*, MV 108*, MV 111*-112*, MV 117*, MV 127*

Rana (Clinotarsus) curtipes Jerdon, 1853. – INDIA: *Thekaddi, Periyar, Tiger Reserve, Kerala*: MNHN 1989 2751

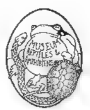
Rana (Hydrophylax) malabarica Tschudi, 1838 INDIA *Bengal* MNHN 4439, 1989 3448, *Malabar* MNHN 771, 4440, 1989.3451-3452

Rana (Sylvirana) gracilis Gravenhorst, 1829. – SRI LANKA *Belihuloya* MNHN 2000.0614

Rana (Sylvirana) temporalis Gunther, 1864 INDIA *Coonoor, Nilghiris* MNHN 1902 0128, *Gundia, Karnataka* MNHN 1985 584-586. – SRI LANKA *Kitulgala*: MNHN 2000 0613.

Sphaerotheca pluvialis (Jerdon, 1853) [valid nomen of the species often referred to as *Rana breviceps* Schneider, 1799 see DUBOIS, 2000, and DUBOIS & OHLER, in preparation] INDIA *Madras* BMNH 1874 4 29*, 1947.2 28 55*-56*, 1947 2 28 58* MSNG 28519* MYANMAR *North Chin Hills* BMNH 1893 11 17 4* NEPAL *Burtmarang* MNHN 1997 5100*-5119*, *Tekunala* MNHN 1983 0808*-0812* PAKISTAN *Lower Hub River* MNHN 9624*, 9626* SRI LANKA BMNH 1877 3 9 8*, *Kurunegala*, 1973.3024*.

Corresponding editor Miguel VENCES



Association des Amis du Laboratoire des Reptiles et Amphibiens du Muséum (AALRAM)

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EXTRAIT DES STATUTS DE L'AALRAM

Les buts de l'association sont de défendre par tous les moyens les intérêts matériels et moraux du Laboratoire de Zoologie (Reptiles et Amphibiens) du Muséum national d'Histoire naturelle, de soutenir son action dans le domaine de l'étude scientifique et de la protection des Reptiles et Amphibiens et de leurs milieux, son rayonnement et l'enrichissement des collections nationales dont il est le dépositaire

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Le nom ***Dumerilia*** est un hommage à la mémoire d'André-Marie-Constant DUMÉRIL (1774-1860), l'un des fondateurs de l'herpétologie, premier auteur du magistral traité intitulé *Erpétologie générale* (1834-1854).

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A new genus for an aquatic ranid (Amphibia, Anura) from Sri Lanka

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A new monotypic genus is erected for the species *Rana corrugata* Peters, 1863, a ranid endemic of the island of Sri Lanka. This species shares the paedomorphic condition of the retention of a lateral-line system in adults with two other genera of Ranidae, *Euphlyctis* and *Occidozyga*. It shares with many species of the genus *Limnonectes* the presence of odontoid "fangs" on the anterior lower jaw of males. Despite these similarities, the new genus is not closely related to the three genera above, and appears to represent a new, independent lineage within the South Indian ranids. It is here provisionally referred to a new subfamily of the family Ranidae. This study provides an opportunity for a brief review of the distribution of several interesting characters among several genera of Ranidae, including characters related with an aquatic mode of life (general morphology, lateral-line system, coloration of the back of thighs), male secondary characters (fangs, large head, dorsal cephalic knob, size dimorphism, nuptial pads, vocal sacs, advertisement and territorial calls), amplectic position, parental care and egg coloration.

Abbreviations

Measurements. EL, eye length; EN, distance from front of eye to nostril; FFTF, distance from maximum incurvation of web between fourth and fifth toe to tip of fourth toe; FL, femur length (from vent to knee); FLL, forelimb length (from elbow to base of outer palmar tubercle); FOL, foot length (from base of inner metatarsal tubercle to tip of fourth toe); HAL, hand length (from base of outer palmar tubercle to tip of third finger); HL, head length (from back of mandible to tip of snout); HW, head width; IBE, distance between back of eyes; IFE, distance between front of eyes; IMT, length of inner metatarsal tubercle; IN, internarial space; ITL, inner toe length; IUE, minimum distance between upper eyelids; MBE, distance from back of mandible to back of eye; MFE, distance from back of mandible to front of eye; MN, distance from back of mandible to nostril; MTFF, distance from distal edge of metatarsal tubercle to maximum incurvation of web between fourth and fifth toe; MTTF, distance from distal edge of metatarsal tubercle to maximum incurvation of web between third and fourth toe; *nm*, no measurement taken; NS, distance from nostril to tip of snout; SL, distance from front of eye to tip of snout; SVL, snout-vent length; TFOL, length of tarsus and foot (from base of tarsus to tip of fourth toe); TFTF, distance from maximum incurvation of web between third and fourth toe to tip of fourth toe; TL, tibia length; TW, maximum tibia width; UEW, maximum width of upper eyelid.

Museums, collections and persons. – AD, Alain Dubois, AMO, Annemarie Ohler; BMNH, Natural History Museum, London, United Kingdom, MNHN, Muséum National d'Histoire Naturelle, Paris, France, MV, Michael Veith collection, Mainz, Germany, NHMB, Naturhistorisches Museum Basel, Basel, Switzerland, NMW, Naturhistorisches Museum, Wien, Austria; NRM, Swedish Museum of Natural History, Stockholm, Sweden, ZMB, Zoologisches Museum, Berlin, Germany

INTRODUCTION

Taxonomy of the family Ranidae Rafinesque-Schmaltz, 1814 is among the most challenging in anuran amphibians. This is due in part to the existence of groups including many sibling species (see e.g.: DUBOIS, 1977, MATSUI et al., 1993, EMERSON & WARD, 1998), and of numerous cases of convergence between species belonging to distinct lineages (see e.g.: OHLER & DUBOIS, 1989; BOSSUYT & MILINKOVITCH, 2000, MARMAYOU et al., 2000)

Particularly confused and controversial is the taxonomy of the so-called genus *Rana* Linnaeus, 1758 (sensu BOULENGER, 1920), that has until now been used to group frogs belonging to various lineages but showing "generalized" morphologies and unspecialized plesiomorphic characters. As far back as in 1915, however, BOLKAY had proposed to remove from this genus several species with a forked omosternum and other unusual characters for the genus *Rana*, and to place them in the new genus *Fejervarya*. A similar proposal was made by DECKERT (1938), followed by LAURENT (1950) and others, who used the generic nomen *Dicroglossus* Günther, 1860 for these frogs: in particular, for several decades, the common African frog now known as *Hoplobatrachus occipitalis* (see e.g. KOSUCH et al., 2001) was referred to under the nomen *Dicroglossus occipitalis*. However, this was ignored by many other authors, especially those working on the Asian fauna (see e.g.: BOURRET, 1942, LIU, 1950, INGER, 1954, 1966, 1985; LIU & HU, 1961; TAYLOR, 1962; etc.). DUBOIS (1974) was the first author to use the nomen *Dicroglossus* for Asian frogs, before showing (DUBOIS, 1975) that this nomen was a strict junior synonym of *Euphlyctis* Fitzinger, 1843. The same author subsequently distributed the ranid species with forked omosternum in several subgenera of *Rana* (DUBOIS, 1981), and later in several distinct genera (DUBOIS, 1987*b*, 1992). Among the five subgenera he recognized in *Limnonectes* Fitzinger, 1843 in 1987, DUBOIS (1992) raised *Hoplobatrachus* Peters, 1863 and *Taylorana* Dubois, 1987 to the rank of distinct genera, and DUBOIS & OHLER (2000) did the same for *Fejervarya*. OHLER & DUBOIS (1999) showed that *Bourretia* Dubois, 1987 was a junior synonym of *Elachyglossa* Andersson, 1916. Therefore, according to these latter authors, the genus *Limnonectes* is now understood as including two subgenera, *Elachyglossa* and *Limnonectes*, the latter with three species-groups (DUBOIS, 1987*b*: 63).

In the genus *Limnonectes*, the *Limnonectes kuhlii* group corresponds to the *Ranae kuhlianae* of BOULENGER (1920). Adult males of these frogs are devoid of vocal sacs and nuptial pads, but have very enlarged heads and strong tooth-like prominences ("fangs") on the anterior lower jaw. All species of this group occur in South-East Asia (Indonesia, Malaysia, Indochina and southern China), except for one, originally described by PETERS (1863) as *Rana corrugata*, which lives only in Sri Lanka. When he first erected the *L. kuhlii* group, DUBOIS (1987*b*) followed BOULENGER (1920) in including this Sri Lankan species in this group, although he had never had an opportunity to examine a specimen of this species.

However, as soon as he first saw this species alive in the field, on 30 June 1999 in Morningside in Sri Lanka, he realized that all published descriptions of this species (Peters, 1863, Günther, 1864; Boulenger, 1882, 1890, 1920; Kirtisinghe, 1957, Dutta & Manamendra-Arachchi, 1996) were incomplete or even partly inaccurate, and that the external characters of this species (see below) were in several respects quite different from those of the *L. kuhlii* group and justified the exclusion of this species not only from this group but also from the genus *Limnonectes*.

Recently, some molecular cladistic data were published concerning these frogs. After an analysis of parts of the mitochondrial ribosomal 12S and 16S genes of several species, Emerson et al. (2000: 136) wrote that "the fanged frogs constitute a monophyletic group" and that "it seems appropriate, in the future, to refer to these frogs as members of the genus *Limnonectes*". While doing so, however, they did not provide a list of taxa that they referred to this genus, so that one can infer that they probably adopted Dubois's (1992) concept of the latter. However, they provided (Emerson et al., 2000: 131) a "definition" of "fanged frogs" that does not apply to all species or species-groups of this genus. All characters listed in this "definition" either apply to some of these taxa only (see e.g. Boulenger, 1920, Dubois, 1987*b*, 1992), such as fangs and "voicelessness" (see below) in adult males, sexual size dimorphism or parental care. However, using this "definition", it is quite clear that *Rana corrugata* should be included in the genus *Limnonectes*. These authors did not, however, consider this species in their study.

Other recent studies provided additional data in this respect. Using mitochondrial 12S and 16S rRNA gene sequences, Vences et al. (2000) and Delorme et al. (submitted) found that *Rana corrugata* is not cladistically a member of the group including *L. kuhlii*, the type-species of *Limnonectes*. Bossuyt & Milinkovitch (2000) found a similar result using the same genes but also two nuclear DNA gene sequences. These data confirm the morphological interpretation of *R. corrugata* as not belonging in the genus *Limnonectes*.

On the basis of the molecular phylogenetic data mentioned above, Delorme et al. (submitted) followed Dubois (1992) in recognizing in the Ranidae a subfamily Dicroglossinae Anderson, 1871, and, within the latter, a tribe Limnonectini Dubois, 1992 for the genera *Limnonectes* and *Taylorana*. They excluded *Rana corrugata* from this tribe, suggesting that the latter deserves erection of a new genus, that represents an hitherto unsuspected new clade within the Ranidae. In the frame of the current "working taxonomy" of the latter family (Dubois, 1999), we suggest that this clade be recognized provisionally as a new subfamily, and we hereby propose a diagnosis and a nomen both for this subfamily and for its unique genus. In order to facilitate the discussion below, we introduce the new nomina first, so that we can use them in the rest of the paper. According to Kelum Manamendra-Arachchi (personal communication), some differences exist between low and high altitude populations currently referred to this species, so that later two distinct taxa (species or subspecies) might have to be distinguished. In order to clarify the nomenclatural decisions that might have to be taken in this respect, we provide a detailed redescription of one of the three original syntypes of this nominal species, that we hereby designate as lectotype. In the final part of the paper, we discuss the distribution of some morphological characters among several genera of Ranidae, that give support to our taxonomic decisions.

Material and methods

The list of specimens examined and measured is given below in tab. 4 and in app. 1.

Twenty-two measurements of adult and young specimens were taken by AMO with a slide calliper to the nearest 0.1 mm, or, for values below 5 mm, with an ocular micrometer to the nearest 0.01 mm. The list of measurements is given above under *Abbreviations*.

In order to facilitate comparisons, the description's methodology and plan used in the lectotype description below were the same as those used in previous works on Asian anurans (Dubois & Ohler, 1998, 1999, 2000; Ohler & Dubois, 1999, Bossuyt & Dubois, 2001; Veith et al., 2001; Dubois et al., 2001). The webbing formula is given according to Myers & Duellman (1982) and the tadpole keratodont formula according to Dubois (1995).

Morphometric analyses and graphs were made using the SPSS statistical programs for personal computers (Norusis, 1992, Anonymous, 1999). We used principal component analysis using varimax rotation (Anonymous, 1999: 426) to show morphological distinctiveness of the new genus and canonical discriminant analysis to indicate morphological discrimination from the subgenera and species-groups of *Limnonectes*. Oneway analysis using Scheffe tests were performed on ranked ratios of all measurements between the seven genera of Ranidae compared in tab. 1. Detailed results of this analysis can be communicated upon request by the authors; they are not provided here because of space limitations.

Taxonomic novelties

Subfamily **Lankanectinae** nov.

Type-genus, by present designation. – *Lankanectes* gen. nov.

Diagnosis. – This subfamily is distinguished from all other subfamilies of Ranidae by the following combination of characters: (1) omosternum forked at base, (2) vomerine teeth present, (3) median lingual process absent, (4) femoral gland absent, (5) extremities of digits pointed or slightly rounded, not enlarged; (6) tarsal fold present; (7) lateral-line system present in adult, (8) head and back covered by a network of ridges, (9) adult male without nuptial pads, but with fangs and internal vocal sacs, (10) eggs pigmented, (11) tadpole with ventral mouthparts, keratodont formula 2/3.

Distribution. – So far, this subfamily is known only from the island of Sri Lanka.

Genus **Lankanectes** nov.

Type-species, by present designation – *Rana corrugata* Peters, 1863.

Diagnosis. – This genus is distinguished from all other genera of Ranidae by the following combination of characters: (1) omosternum forked at base; (2) size medium (adult SVL 33-65 mm); (3) internarial distance shorter than distance between upper eyelids; (4) upper eyelids covered with numerous round warts; (5) canthus rostralis indistinct, loreal region slightly convex; (6) edge of lower jaw without transverse bands; (7) tympanum indistinct; (8) vomerine teeth present, (9) median lingual process (see GRANT et al., 1997) absent, (10) extremities of fingers pointed, of toes slightly rounded; (11) finger II longer than finger I; (12) no distal subarticular tubercles on fingers III and IV; (13) inner palmar tubercle very small, rounded, on base of metacarpus, (14) outer palmar tubercle very small, rounded, similar and of same size as inner; (15) legs strong, heels far apart when hind legs are placed at right angle with body, (16) tarsal fold present, well developed, (17) inner metatarsal tubercle flat, elongate, (18) outer metatarsal tubercle absent; (19) tarsal tubercle absent; (20) femoral glands absent; (21) lateral-line system present in adult, (22) dorsal parts covered with a network of ridges, (23) fejervaryan line (see DUBOIS & OHLER, 2000, and DUBOIS et al., 2001) absent; (24) rear part of thighs marbled, without longitudinal white and dark lines; (25) adult male with fangs and internal vocal sacs, without nuptial pads, (26) eggs pigmented, (27) tadpole with ventral mouthparts, keratodont formula 2/3

Comparisons. Detailed comparisons of this genus with six other genera of Asian Ranidae with forked omosternum are provided in tab. 1. Of particular relevance are the comparisons with three of them, which in several characters rather closely resemble the new genus. *Lankanectes* shares several characters with the Asian ranid genera *Euphlyctis* and *Occidozyga* Kuhl & Van Hasselt, 1822; in particular, in these three genera a lateral line system is present on the body of adults, a rare character in the Ranidae (see below). It is distinguished from these two genera by a combination of characters (see tab. 1), among which the following ones in particular may be highlighted: (1) internarial distance shorter than distance between upper eyelids (instead of subequal or longer); (2) loreal region slightly convex (instead of slightly concave); (3) network of numerous transverse folds on the whole of back and head (absent in the other two genera); (4) inner metatarsal tubercle flat (instead of digit-like), (5) rear part of thighs marbled (instead of showing a longitudinal white line underlined by a dark line), (6) adult male with fangs on the anterior lower jaw. This last character is shared by the new genus and some species of the genus *Limnonectes*, but *Lankanectes* differs from the latter in several other characters (see tab. 1), including. (1) internarial distance shorter than distance between upper eyelids (instead of subequal or longer), (2) loreal region slightly convex (instead of concave); (3) network of numerous transverse folds on the whole of back and head (absent in *Limnonectes*), (4) upper eyelids covered with numerous round warts (instead of bearing only a few round warts in their rear part), (5) finger II longer than finger I (instead of shorter or subequal), (6) lateral line system present in adult (instead of absent)

Generic content and distribution - For the time being, a single species, *Lankanectes corrugatus* (Peters, 1863), an endemic of the island of Sri Lankan, is known in this genus. However, as mentioned above, this species might prove later to be heterogeneous and to consist in fact of

Table 1. Some diagnostic morphological characters of seven Asian genera of the family Ranidae with omosternum forked at base. See DUBOIS (1995) for the definition of the tadpole's condensed collective keratodont formula (CCKF), i.e. minimum-maximum numbers of keratodont rows on upper/lower lips of tadpoles observed in the taxon. See OHLER & DUBOIS (1999) for the definition of categories of digital disks in the Ranidae.

Subfamily	Dicroglossinae Anderson, 1871	Dicroglossinae Anderson, 1871	Dicroglossinae Anderson, 1871	Occidozyginae Fei, Ye & Huang, 1991	Occidozyginae Fei, Ye & Huang, 1991	Nyctibatrachinae Blommers-Schlösser, 1993	Lankanectinae subfam. nov.
Tribe	Dicroglossini Anderson, 1871	Limnonectini Dubois, 1992	Limnonectini Dubois, 1992		–		
Genus	*Euphlyctis* Fitzinger, 1843	*Limnonectes* Fitzinger, 1843	*Taylorana* Dubois, 1987	*Occidozyga* Kuhl & Van Hasselt, 1822	*Phrynoglossus* Peters, 1867	*Nyctibatrachus* Boulenger, 1882	*Lankanectes* gen. nov.
Type-species	*Rana leschenaultii* Duméril & Bibron, 1841 by original designation (FITZINGER, 1843: 31)	*Rana kuhlii* Tschudi, 1838, by original designation (FITZINGER, 1843: 31)	*Polypedates hascheanus* Stoliczka, 1870, by original designation (DUBOIS, 1987*b*: 63)	*Rana lima* Gravenhorst, 1829, by subsequent designation of STEJNEGER (1925: 13)	*Phrynoglossus martensii* Peters, 1867, by original monotypy (PETERS, 1867: 29)	*Nyctibatrachus major* Boulenger, 1882, by subsequent designation of MYERS (1942: 54)	*Rana corrugata* Peters, 1863, by original designation (hoc loco)
Adult male SVL (mm)	40-95	35-150	25-39	19-26	18-30	3-46	33-65
Adult female SVL (mm)	45-130	35-135	24-37	26-35	22-45	14-47	44-59
Internarial distance	Longer than distance between upper eyelids	Longer than or equal to distance between upper eyelids	Longer than distance between upper eyelids	Subequal to distance between upper eyelids	Longer than distance between upper eyelids	Shorter than distance between upper eyelids	Shorter than distance between upper eyelids
Upper eyelids	Covered with numerous round warts	Bearing a few round warts in their rear part	Bearing a few round warts in their rear part	Covered with numerous round warts	Covered with a few indistinct round warts	Without wards or covered with numerous round warts	Covered with numerous round warts
Canthus rostralis	Indistinct	Distinct or little distinct	Little distinct	Indistinct	Indistinct	Indistinct or little distinct	Indistinct
Loreal region	Slightly concave	Concave	Flat	Slightly concave	Slightly convex	Slightly convex	Slightly convex
Coloration of edge of lower jaw	Without transverse bands	With transverse bands	With transverse bands	Without transverse bands	Without transverse bands	Without transverse bands	Without transverse bands
Tympanum	Distinct	Distinct or indistinct	Distinct	Indistinct	Indistinct	Indistinct or little distinct	Indistinct
Extremities of digits	Pointed, not enlarged	Rounded, those of toes sometimes dilated as small disks bearing a dorso-terminal fold	Slightly enlarged with a rudimentary dorso-terminal fold	Pointed, not enlarged	Rounded, sometimes slightly enlarged	Disks bearing dorso terminal folds	Extremities of fingers pointed, or toes slightly rounded
Relative length of fingers I and II	Finger II longer than finger I	Finger II shorter than or as long as finger I	Finger II shorter than finger I	Fingers I and II subequal	Finger II shorter than finger I	Finger II longer than finger I	Finger II longer than finger I
Distal subarticular tubercles on fingers III and IV	Small	Indistinct	Small	Absent	Absent	Indistinct	Absent
Inner palmar tubercle	Medium, oval, on the base of metacarpus	Medium or large, on base of metacarpus or on the whole of it	Medium, oval, on half of metacarpus	Small, rounded, prominent, on base of metacarpus	Small, oval, on base of metacarpus	Small, oval, rather prominent, on base of metacarpus	Very small, rounded, on base of metacarpus
Outer palmar tubercle	Indistinct	Elongate, half smaller than inner palmar tubercle or of same size	Oval, a little smaller than inner	Small, rounded prominent, of same size as inner palmar tubercle	Small, oval, of same size as inner palmar tubercle	Oval, about half-size of inner palmar tubercle	Very small, rounded, of same size as inner palmar tubercle

Table 1 (continued)

Genus	*Euphlyctis* Fitzinger, 1843	*Limnonectes* Fitzinger, 1843	*Taylorana* Dubois, 1987	*Occidozyga* Kuhl & Van Hasselt, 1822	*Phrynoglossus* Peters, 1867	*Nyctibatrachus* Boulenger, 1882	*Lankanectes* gen. nov.
Hind legs	Rather strong and short	Strong or narrow, short or long	Moderately strong, rather short	Rather strong, short	Rather strong, short	Strong, short	Very strong, short
Distance between heels when hind legs are placed at right angle with body	Heels far apart	Heels in contact or overlapping	Heels in contact	Heels far apart	Heels far apart	Heels far apart	Heels far apart
Tarsal fold or ridge	Present, moderate	Present, well developed	Indistinct	Present, moderate	Present, well developed	Present, well developed	Present, well developed
Inner metatarsal tubercle	Finger-like, elongate	Flat, elongate	Very prominent, elongate	Finger-like, very prominent	Oval, very prominent	Long, oval, prominent	Flat, elongate
Outer metatarsal tubercle	Absent	Absent	Absent	Present	Absent	Absent	Absent
Tarsal tubercle	Absent	Absent	Absent	Present	Absent	Absent	Absent
Femoral glands	Absent	Absent	Absent	Absent	Absent	Present	Absent
Lateral line system in adult	Present	Absent	Absent	Present	Absent	Absent	Present
Longitudinal dorsal glandular folds	Absent	Present or absent	Present	Absent	Absent	Absent	Absent
Network of ridges on back and head	Absent	Absent	Absent	Absent	Absent	Absent	Present
Coloration of rear part of thighs	Longitudinal white line underlined by dark line	Marbled	Marbled	Longitudinal white line underlined by black line	Marbled or spotted	Marbled	Marbled
Sex size dimorphism	Males smaller than females	Absent or males larger than females	Absent	Males smaller than females	Males smaller than females	Absent	Absent
Enlargement of head in adult male	Absent	Present or absent	Present	Absent	Absent	Absent	Absent
Fangs in adult male	Absent	Present or absent	Present, small	Absent	Absent	Absent	Present
Vocal sacs in adult male	Present, black, protruding through slits on ventral sides on throat	Absent or present, internal, with folds on throat	Absent	Present, internal, with folds on throat	Present, internal with folds on throat	Present, internal, with folds on throat	Present, internal, without folds on throat
Male advertisement call	Present	Absent or present	Present	Present	Present	Present	Present
Nuptial pads in adult male	Absent	Absent	Absent	Present	Present	Present	Absent
Amplectic position	Axillary	?	?	Axillary	Lumbar	?	?
Egg coloration	Pigmented	Pigmented	Unpigmented	Pigmented	Unpigmented	Pigmented or not	Pigmented
Mode of development	Tadpole	Tadpole or endotroph	Endotroph	Tadpole	Tadpole	Tadpole	Tadpole
Parental care	Absent	Absent or present	Present	Absent	Absent	Absent	Absent
Tadpole's CKF	2	-3 -3	-	0/0	0/0	0/0	2/3
References for characters	BOULENGER, 1920; DECKERT, 1938; DUBOIS, [illegible]	BOULENGER, 1920; DECKERT, 1938	BOULENGER, 1920; TAYLOR, 1962; YANG, 1991; OHLER et al., 1999	BOULENGER, 1890; DECKERT, 1938; YANG, 1991	DECKERT, 1938; INGER, 1966; YANG, 1991	CLARKE, 1983; INGER et al., 1984	BOULENGER, 1920; DECKERT, 1938; KIRTISINGHE, 1957; DUTTA & MANAMENDRA-ARACHCHI, 1996

two species or subspecies. In order to facilitate further works in this respect, we provide below a detailed redescription of the lectotype, designated herein, of *Rana corrugata* Peters, 1863

Vernacular name We propose to use the name "lankanects" as vernacular name for these frogs, and "limnonects" for frogs of the genus *Limnonectes*.

Etymology of the generic nomen – The new generic nomen, of masculine grammatical gender, is derived from the frog generic nomen *Limnonectes* Fitzinger, 1843, and from the name of the island of Sri Lanka It suggests that these frogs are limnonect-like frogs endemic of this island

Lectotype description

Lectotype, by present designation, of *Rana corrugata* Peters, 1863: ZMB 4897, adult male (fig. 1), collected by J. Nietner in "Rambodde" (Ramboda; 07°03'N, 80°14'E; 1310 m) (Dutta & Manamendra-Arachchi, 1996: 12), Sri Lanka.

(A) Size and general aspect. (1) Specimen of moderate size (SVL 44 0 mm), body stout

(B) Head. (2) Head rather large, wider (HW 17.2 mm) than long (HL 16.8 mm, MN 15.3 mm; MFE 12 8 mm; MBE 8 3 mm), convex (3) Snout rounded, slightly protruding; its length (SL 6 03 mm) longer than horizontal diameter of eye (EL 5.25 mm). (4) Canthus rostralis indistinct, loreal region convex; angle of loreal region with upper face of head flared (5) Interorbital space flat, broader (IUE 4.02 mm) than upper eyelid (UEW 2.01 mm) and than internarial distance (IN 2.46 mm); distance between front of eyes (IFE 6 68 mm) about half of distance between back of eyes (IBE 12 76 mm) (6) Nostrils oval, with small flap of skin laterally; closer to eye (EN 2.66 mm) than to tip of snout (NS 3.37 mm). (7) Pupil not observable. (8) Tympanum indistinct (TYD *nm*, TYE *nm*) (9) Pineal ocellus absent (10) Maxillary teeth present; vomerine ridge present, bearing 2 small teeth, posterior to choanae, with an angle of 40° relative to body axis, closer to each other than to choanae, longer than distance between them (11) Tongue chordate, deeply emarginate, without lingual process, covered by numerous small papillae (12) A dermal, non glandular supratympanic fold, distinct, from eye to shoulder (13) Parotoid glands absent (14) Cephalic ridges absent (15) Co-ossified skin absent.

(C) Forelimbs. (16) Arm short, fore-arm (FLL 8.6 mm) shorter than hand (HAL 8 8 mm), not enlarged. (17) Fingers short and rather strong (TFL 4 21 mm). (18) Relative length of fingers, shortest to longest I < IV < II < III (19) Tips of fingers pointed, bearing small, rounded terminal notch, not enlarged (20) Fingers without dermal fringe and webbing (21) Subarticular tubercles prominent, conical, single; distal tubercle of finger III and IV absent (22) Prepollex small (size of subarticular tubercles), rounded, distinct; a single, small, round inner palmar tubercle on the base of metacarpus, outer palmar tubercle similar and of same size as inner; supernumerary tubercles absent.

(D) Hindlimbs. (23) Shank two times longer (TL 18 7 mm) than wide (TW 10.1 mm), shorter than thigh (FL 19 7 mm) and than distance from base of internal metatarsal tubercle to tip of toe IV (FOL 19 8 mm) (24) Toes short, rather thin, toe IV (FTL 10.8) longer than third of distance from base of tarsus to tip of toe IV (TFOL 28 5 mm) (25) Relative length of

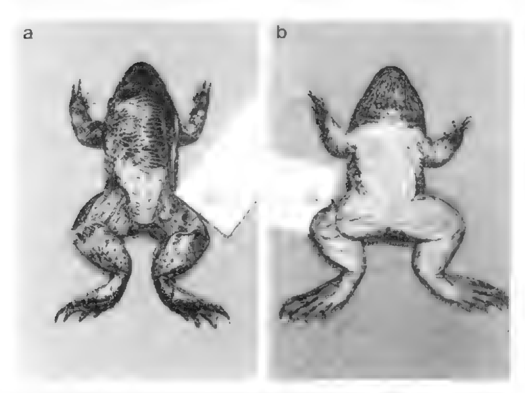


Fig. 1 Lectotype of *Rana corrugata* Peters, 1863, ZMB 4897, adult male (SVL 44.0 mm). (a) Dorsal view. (b) Ventral view

toes, shortest to longest: I < II < V < III < IV (26) Tips of toes pointed, bearing enlarged knob terminally. (27) Webbing complete: I 0 - 0 II 0 – 0 III 0 – 0 IV 0 – 0 V (WTF 7.24 mm; WFF 6.32 mm; WI 6.58 mm; WII 5.00 mm, MTTF 13.68 mm; MTFF 14.47 mm; TFTF 5.66 mm, FFTF 8.42 mm). (28) Dermal fringe along toe V absent. (29) Subarticular tubercles conical, all present. (30) Inner metatarsal tubercle elongate, very prominent, shovel-shaped, its length (IMT 3.18 mm) 2 times in length of toe I (ITL 6.35 mm). (31) Tarsal fold present, from inner metatarsal tubercle to before tibio-tarsal articulation. (32) Outer metatarsal tubercle, supernumerary tubercles and tarsal tubercle absent.

(E) Skin. (33) Dorsal and lateral parts of head and body: smooth skin forming numerous regularly arranged folds, transversally arranged on back, longitudinally arranged between eyes; between these folds presence of round indistinct warts; laterally on posterior part of back, 4-5 symmetrically arranged pairs of prominent, medium sized warts, flanks smooth. (34) Latero-dorsal folds absent. (35) Dorsal parts of limbs: forelimb with transversal foldings; thigh with flat warts, leg and tarsus with glandular warts bearing horny spinules. (36) Ventral parts of head, body and limbs: throat with longitudinal foldings, chest, belly and thigh smooth, fejervaryan line absent, lateral-line system indistinct. (37) Macroglands absent.

(F) Coloration in alcool. — (38) Dorsal and lateral parts of head and body: dorsal parts of head and dorsum and upper part of flank dark brown with top of folds whitish (discoloration), a blackish brown band between eyes. (39) Dorsal parts of limbs: dorsal part of forelimb, of thigh, of shank and of foot dark brown with indistinct darker brown bands, posterior part of thigh brown with blackish triangle around vent. (40) Ventral parts of head, body and limbs: throat and margin of throat dark brown; chest and belly whitish with some dark brown spots; thigh whitish; webbing whitish with dark brown marblings.

(G) Male secondary sexual characters. — (41) Nuptial spines absent. (42) Vocal sacs present, indistinct on throat; distinct, rounded, paired openings, posteriorly on mouth floor. (43) Other male secondary sexual characters: toothlike projections (fangs) at the front of lower jaw.

Discussion

Morphological and morphometric analyses

Morphological comparison between the genus *Lankanectes* and 6 other genera of Asian Ranidae with omosternum forked at base is given in tab. 1. Some of the major differences between the new genus and these genera were already mentioned in the diagnoses of the new taxa given above, and are not repeated here.

Morphometric comparisons also support the distinctiveness of the new taxon. As we have already stressed elsewhere (e.g., Dubois et al., 2001), in many anuran groups the general "body shape" gives good clues regarding generic classification and allocation of species to genera. Once again we confirm this statement in the present study. On the basis of 22 measurements (see *Material and methods* above), we compared *Lankanectes corrugatus* with several species belonging to the four subgenera and species-groups currently recognized in the genus *Limnonectes*. Besides, we also thought useful to compare this species with members of several other genera discussed above (*Euphlyctis*, *Occidozyga* and *Phrynoglossus*) and also with the genus *Nyctibatrachus*, an endemic of southern India. The results are shown in tab. 2 and fig. 2. *Lankanectes corrugatus* appears as a well-distinguished group, as much as the other genera considered here. This result is confirmed by the canonical discriminant analysis based on 19 measurements and involving *Lankanectes* and the four subgroups (subgenera or species-groups) currently recognized in the genus *Limnonectes* (tab. 3, fig. 3).

Oneway analysis using the Scheffe test shows significant differences in various characters between *Lankanectes* specimens and specimens of the 8 other taxa studied. The new genus can be distinguished from all 4 subgroups of *Limnonectes* studied by a shorter head (HL), shorter eye-nostril distance (EN) and shorter shank (TL). Members of the subgenus *Elachyglossa* also have larger head (HW), greater internarial distance (IN) and more developed webbing (TFTF). The frogs of the *grunniens* species-group are significantly larger (SVL) than *Lankanectes* specimens and show differences in eye position (MFE, IBE). As compared to the *kuhlii* species-group, the new genus has significantly smaller (HW) and shorter head (beside HL, MN is significantly shorter), shorter forearm (FLL) and less developed webbing (MTFF).

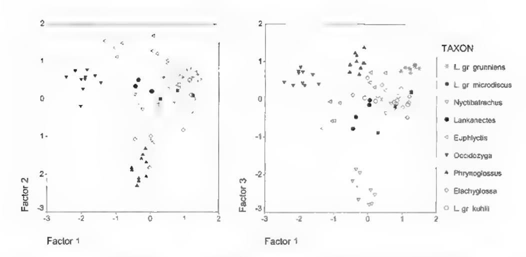


Fig. 2. Plots of multivariate analysis (first three axes) based on 22 measurements for the following nine genera, subgenera and species-groups of Asian Ranidae *Euphlyctis*, *Lankanectes*, *Limnonectes (Elachyglossa)*, *Limnonectes (Limnonectes)* gr. *grunniens*, *Limnonectes (Limnonectes)* gr *kuhlii*, *Limnonectes (Limnonectes)* gr. *microdiscus*, *Nyctibatrachus*, *Occidozyga* and *Phrynoglossus*.

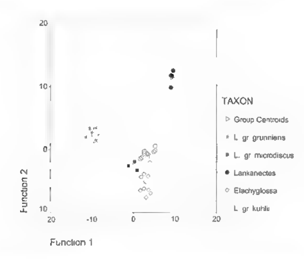


Fig 3. Plots of discriminant function scores using minimization of Wilk's lambda of morphometric log-transposed characters (19 measurements) for the following five genera, subgenera and species groups of Asian Ranidae *Lankanectes*, *Limnonectes (Elachyglossa)*, *Limnonectes (Limnonectes)* gr *grunniens*, *Limnonectes (Limnonectes)* gr *kuhlii* and *Limnonectes (Limnonectes)* gr *microdiscus*.

Table 2. - Results of principal component analysis based on 22 ln-transposed measurements including specimens referred to the genera *Euphlyctis*, *Lankanectes*, *Limnonectes*, *Nyctibatrachus*, *Occidozyga*, and *Phrynoglossus*.

Component	Initial Eigenvalues			Rotation Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	19.991	90.870	90.870	10.520	47.819	47.819
2	1.148	5.219	96.089	7.154	32.518	80.338
3	0.260	1.181	97.270	3.725	16.932	97.270

Variable	Components for rotated component matrix			Variable	Components for rotated component matrix		
	1	2	3		1	2	3
SVL	0.670	0.635	0.374	FOL	0.630	0.623	0.427
HW	0.719	0.599	0.333	IN	0.951	0.230	0.132
HL	0.711	0.608	0.341	EN	0.699	0.571	0.397
MN	0.697	0.593	0.383	EL	0.702	0.605	0.460
MFE	0.698	0.583	0.388	TFL	0.564	0.720	0.366
MBE	0.605	0.596	0.468	MTTF	0.475	0.692	0.525
IFE	0.838	0.451	0.286	TFTF	0.814	0.497	0.334
IBE	0.831	0.504	0.165	MTFF	0.452	0.713	0.520
FLL	0.743	0.569	0.334	FFTF	0.852	0.405	0.208
HAL	0.589	0.694	0.392	IMT	0.700	0.483	0.460
TL	0.706	0.590	0.374	ITL	0.108	0.283	0.949

Specimens of the *microdiscus* species-group have a larger distance between eyes (IFE) and nostrils (IN) and their webbing is more incurved (TFTF). As to the differences existing to the other genera studied here, *Lankanectes* is larger (SVL) than *Nyctibatrachus*, its notrils are more distantly separated; the inner metatarsal tubercle is smaller (IMT) in *Nyctibatrachus*, as is the webbing of the feet (MTTF, MTFF, TFTF). *Phrynoglossus* can be distinguished from the new genus by its smaller body size (SVL), its larger internarial distance (IN), its larger inner metatarsal tubercle (IMT) and its smaller webbing (MTFF, TFTF). Members of the genus *Occidozyga* show smaller distance between the eyes (IBE), longer hand length (HAL), a shorter inner metatarsal tubercle (IMT) and a longer inner toe (ITL). A smaller distance between the eyes and a smaller inner metatarsal tubercle separates *Lankanectes* from the members of the genus *Euphlyctis*.

Table 3. Results of principal component analysis based on varimax rotated coefficients from log-transposed characters (25 measurements) for specimens referred to the genera *Euphlyctis*, *Fejervarya*, *Hoplobatrachus*, *Limnonectes*, *Minervarya* and *Sphaerotheca*.

	Initial Eigenvalues		
Component	Total	% of Variance	Cumulative %
1	22.639	90.558	90.558
2	0.799	3.196	93.754
3	0.696	2.783	96.537

	Rotation Sums of Squared Loadings		
Component	Total	% of Variance	Cumulative %
1	10.152	40.610	40.610
2	9.597	38.390	78.999
3	4.384	17.538	96.537

	Components for rotated component matrix		
Variable	1	2	3
SVL	0.649	0.621	0.422
HW	0.617	0.706	0.337
HL	0.673	0.647	0.340
MN	0.667	0.646	0.330
MFE	0.649	0.674	0.322
MBE	0.639	0.683	0.312
IFE	0.505	0.768	0.371
IBE	0.553	0.757	0.368
FLL	0.589	0.682	0.419
HAL	0.661	0.653	0.346
TL	0.732	0.530	0.410
FOL	0.709	0.534	0.456
IN	0.235	0.817	0.471
EN	0.698	0.592	0.353
EL	0.599	0.691	0.351
TYD	0.712	0.487	0.367
TYE	0.449	0.773	0.223
TFL	0.654	0.635	0.364
FTL	0.757	0.415	0.484
MTTF	0.836	0.453	0.299
IFTF	0.349	0.349	0.859
MTFF	0.830	0.463	0.297
FFTF	0.432	0.402	0.788
IMT	0.419	0.797	0.293
ITL	0.873	0.304	0.283

Table 4. Some measurements and ratios of four specimens of *Lankanectes corrugatus*, including the lectotype (ZMB 4897) and the two paralectotypes (ZMB 62771-62772) from Rambodde (Sri Lanka), and a fourth specimen (MNHN 2000.0616) from Kandy (Sri Lanka). SVL is given in mm, all other measurements are given as per thousands of SVL. Sex and stages: A, adult; J, juvenile; F, female; M, male.

Collection number	ZMB 4897	ZMB 62771	ZMB 62772	MNHN 2000.0616
Locality	Rambodde	Rambodde	Rambodde	Kandy
Sex and stage	AM	JF	AM	AF
SVL	44.0	37.2	33.5	44.4
HW	391	363	337	338
HL	382	379	379	354
MN	348	333	333	302
MFE	291	280	280	243
MBE	189	177	177	164
IFE	152	153	153	158
IBE	290	298	298	264
IN	56	70	66	66
EN	60	70	66	70
EL	119	138	106	108
FLL	195	210	185	191
HAL	200	199	224	218
TFL	96	127	120	115
TL	425	414	394	405
FOL	457	465	421	462
FTL	245	242	242	248
IMT	72	63	79	77
ITL	144	148	132	150
MTTF	311	328	310	296
MTFF	329	336	310	329
TFTF	129	124	141	139
FFTF	191	177	189	184

Distribution of some characters among several genera of Ranidae

Characters related with an aquatic mode of life

All anuran tadpoles show a lateral-line system on body and head, similar to that of fishes, i.e. composed of rows of small pores opening on sense cells or neuromasts that are sensible to vibrations of low frequency in water (Noble, 1931: 318-321; Duellman & Trueb, 1985:

378-379). Most anuran species lose this system at metamorphosis, but it remains present in adults of a few anuran groups that have a mainly aquatic mode of life. This retention of a larval character in otherwise adult specimens is a case of partial paedomorphism (DUBOIS, 1987*a*). This is observed in several aquatic genera of anurans, distributed in various families, including the Discoglossidae (*Barbourula* Taylor & Noble, 1924, *Bombina* Oken, 1816), the Leptodactylidae (*Lepidobatrachus* Budgett, 1899) and the Pipidae (all genera) (fig. 4). In the Ranidae, which include various aquatic groups, some of them show the paedomorphic retention of lateral-line systems in adults, while others, which may seemingly appear as aquatic as the former ones, do not show this phenomenon. Three genera of Ranidae are known to retain the lateral-line system in adults: *Euphlyctis* (see e.g.: BOULENGER, 1920; DUBOIS, 1987*b*, 1992), *Occidozyga* Kuhl & Van Hasselt, 1822 (see e.g. DUBOIS, 1987*b*, 1992) and the new genus *Lankanectes* (fig. 4). To the best of our knowledge, the presence of a lateral-line system in adults of *L. corrugatus* has never been mentioned in the scientific literature, although these lines are quite obvious in live specimens (AD, personal observations) and usually remain visible, although not so easily, in fixed specimens.

DUBOIS (1987*b*) had considered the presence of a lateral-line system in adults as a synapomorphy of *Euphlyctis* and *Occidozyga*, which had led him to regard these two taxa as sister-groups and to treat them as subgenera of a single genus. Other characters which had supported this interpretation were the general body shape (*O. lima* looking almost exactly as a miniaturized *E. cyanophlyctis*), the shapes of the foot and of the extremities of digits, and the presence of continuous longitudinal white and dark stripes all along the rear part of the thighs (fig. 5). However, molecular cladistic data provided by MARMAYOU et al. (2000), KOSUCH et al. (2001) and DELORME et al. (submitted) strongly suggest that *Occidozyga* and *Euphlyctis* are not sister-groups, and that all or most of the characters listed above are convergences related to aquatic life. As a matter of fact, as mentioned above the lateral-line system is retained in adults of several aquatic frogs of other families and this is the case also of pointed digits and of fully webbed feet with a relatively short fourth toe.

As concerns the last character of the list above, the presence of longitudinal white and dark stripes on the posterior thigh is also observed in aquatic South-American hylid frogs of the genus *Pseudis* Wagler, 1830 (fig. 5) and, although less strikingly, in Chinese Ranidae that are also largely aquatic, i.e. *Rana (Pelophylax) plancyi* Lataste, 1880 and *Rana (Pelophylax) hubeiensis* Fei & Ye, 1982 (see e.g.: POPE, 1931: 511; FEI, 1999: 161). The meaning of this coloration character is not quite clear, but the fact that it appeared independently in several unrelated anuran groups having a largely aquatic life suggests that it also has an adaptive value for frogs with such a mode of life, probably as a camouflage device towards aquatic or aerial potential predators. In terrestrial frogs that live in grassland habitats, a striped dorsal pattern is often observed. These frogs have longitudinal lines either all along the middle of the back (vertebral stripe or band, present in many groups of frogs), or as several subparallel dark stripes on a brown dorsum. The latter, although perhaps less common, is also a rather widely distributed phenotype in frogs, observed e.g. in the Hyperoliidae (e.g., some *Afrixalus* Laurent, 1944 or *Hyperolius* Rapp, 1842), in the Ranidae (e.g., some *Ptychadena* Boulenger, 1917 or *Strongylopus* Tschudi, 1838), or in the Rhacophorinae/dae (e.g., some *Chirixalus* Boulenger, 1893 or *Polypedates* Tschudi, 1838). Such patterns can clearly contribute to a camouflage among herbs or elongated leaves. However in such frogs the rear parts of the thighs do not show longitudinal stripes. In terrestrial frogs the legs are not kept extended at

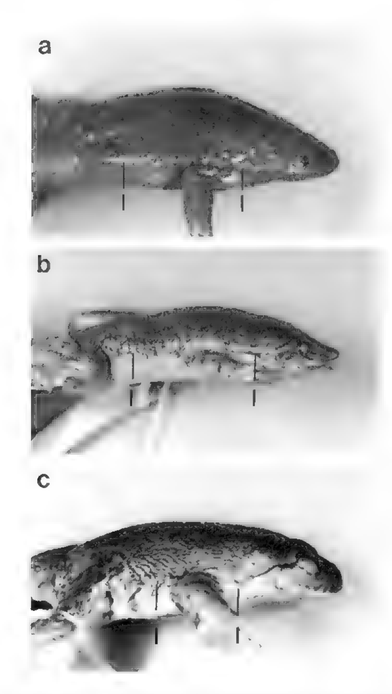
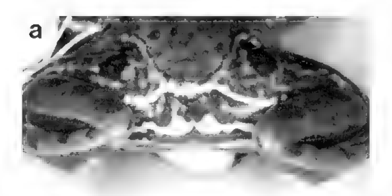


Fig. 4. – Lateral-line system (l) in several examples of aquatic anurans. (a) *Silurana tropicalis* Gray, 1864 (Pipidae, Siluraninae), MNHN 1994.1915, adult male, Guinea. (b) *Occidozyga lima* (Gravenhorst, 1829) (Ranidae, Occidozyginae), MNHN 1999.6418, adult female, Yunnan. (c) *Lankanectes corrugatus* (Peters, 1863), MNHN 2000.0616, adult female, Sri Lanka.



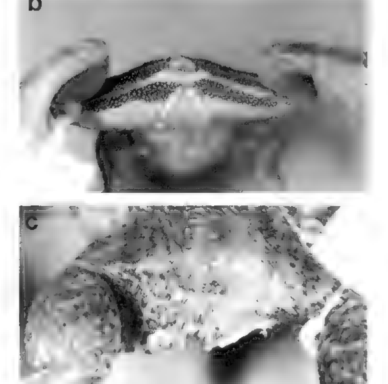


Fig. 5. — Presence and absence of longitudinal white and dark lines on the back of thighs in several examples of aquatic anurans. (a) *Pseudis paradoxus* (Linnaeus, 1758) (Hylidae, Pseudinae), MNHN 1983.0390, juvenile female, Venezuela: lines present. (b) *Occidozyga lima* (Gravenhorst, 1829) (Ranidae, Occidozyginae), MNHN 1999.6418, adult female, Yunnan: lines present. (c) *Lankanectes corrugatus* (Peters, 1863) (Ranidae, Lankanectinae), MNHN 2000.0616, adult female, Sri Lanka: lines absent.

rest, so that the coloration of the back of thighs is not exposed: it is shown only during movements. In aquatic frogs, the situation may be different. These frogs, like *Euphlyctis* or *Occidozyga*, often remain suspended floating in water for some minutes or more, using the four limbs extended in the prolongation of the body or feebly bended laterally as balancers. In such a position the posterior surface of hindlegs is visible. If such a frog is then hidden within long and narrow aquatic vegetal structures, the longitudinal lines at the back of thighs might contribute to the camouflage, especially if it follows some other linear structures or coloration on the flank or dorsum of the frog, as well exemplified in the figure 16 of Pope (1931: 511). Although the new genus *Lankanectes* shares with *Occidozyga* and *Euphlyctis* the retention of lateral-line system in adults, it does not show the longitudinal stripes on the rear parts of the thighs (fig. 5) and this is a significant difference between the two genera (as well as between the closely related *Occidozyga* and *Phrynoglossus*). Perhaps this is connected to the fact that *L. corrugatus* usually inhabits shallow, mud-substrate (as opposed to gravel- or rock-substrate) streams, poor in vegetation (Pethiyagoda, personal communication).

Male secondary sex characters

Anurans display a large diversity of male secondary sex characters, including various kinds of spines, asperities and glands, vocal sacs and adult morphometric differences. The taxonomic significance of such dimorphic characters has no generality over the whole of anurans. In several groups, male secondary sex characters are diagnostic of species-groups, subgenera or genera, or even of higher taxa. this is e.g. the case of the pectoral plates of the megophryid tribe Oreolalagini (see Delorme & Dubois, 2001). In some other cases however, differences in such characters are species-specific and can even separate very similar and closely related species: examples include the presence/absence of nuptial spines in *Paa liebigii* (Günther, 1860) and *Paa vicina* (Stoliczka, 1872) (Dubois, 1976*a*, 1980) and the presence/absence of vocal sacs in *Polypedates leucomystax* (Gravenhorst, 1829) and *Polypedates mutus* (Smith, 1940) (Smith, 1940; Liu & Hu, 1961).

The major reason, besides general morphological resemblance, that apparently led Boulenger (1920) to include *Rana corrugata* in the same group as *Rana kuhlii* seems to have been the presence in both species of "fangs" at the front of the lower jaw (fig. 6). This character was also used by Emerson & Ward (1998) and Emerson et al. (2000) as the basis for the vernacular name of "fanged frogs" which they gave to the genus *Limnonectes*. However, not all frogs of this group possess fangs (see e.g., Boulenger, 1920, Smith, 1922*a-b*, Bourret, 1942), and this vernacular name does not appear more appropriate for these frogs than that of "voiceless frogs", the previous name used by the same authors (Emerson & Voris, 1992, Emerson & Berrigan, 1993). As a matter of fact, even if several species of South-East Asian frogs of this group are devoid of structurally differentiated vocal sacs, they are not voiceless, as their males can emit advertisement calls, as was observed in *Limnonectes blythii* (Matsui, 1995), or at least loud territorial calls, as was observed in *Limnonectes* cf. *kuhlii* (AD & AO, unpublished observations, see below). As for *Lankanectes corrugatus*, males show differentiated vocal sacs and emit loud calls (AD, personal observations, Sri Lanka, June 1999) whose function has to be clarified, given that they persist after the breeding season (Pethiyagoda, personal communication), but which probably can have an advertisement function, possibly combined with a territorial one.

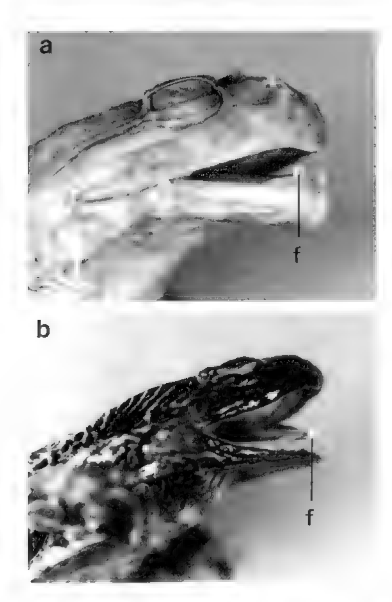


Fig. 6. Fangs (f) at front of lower jaw in two Asian ranid groups. (a) *Limnonectes* (*Limnonectes*) cf. *kuhlii* (Tschudi, 1838) (Ranidae, Dicroglossinae), MNHN 1938.0030, adult male, Vietnam; (b) *Lankanectes corrugatus* (Peters, 1863) (Ranidae, Lankanectinae), ZMB 4897, adult male, lectotype, Sri Lanka.

As mentioned above, fangs are present in adult males of some species of *Limnonectes* only. These species also tend to have a much wider head in males than in females, and in some of them (some of the members of the subgenus *Elachyglossa*) they also show a knob on the dorsal back of head, starting between the eyes and extending beyond them (SMITH, 1922*a-b*;

BOURRET, 1942). We regard all these characters (fangs, wide head, dorsal cephalic knob) as related to agonistic behaviour between males, like in several other cases of spines and other differentiated structures on the heads of males (see e.g.: SHINE, 1979; DUBOIS & OHLER, 1998). In the Siriphum agricultural station of the Doi Inthanon in northern Thailand, in the night of 24 September 1986 we had the opportunity to observe an adult male of *Limnonectes* cf. *kuhlii* that, disturbed by our foraging in water with a small net to collect tadpoles, suddenly emitted a loud and deep territorial call, "*koaa, koaa*", and repeated it several times. While emitting this guttural whistling, this frog had its body immersed in water but its head was raised above the water level, and quite voluntary so as the frog was leaning on a rock and the fore part of its body was raised on its stretched arms. Seen from the level of the surface of water, this large head evoked a much larger frog than the actual size of this male (MNHN 1987.3197, SVL 63.7 mm; HW 28.6 mm, HL 29.6 mm). On several occasions, in Thailand, Laos and Vietnam, we had the opportunity to observe and collect very large-headed males of *Limnonectes* cf. *kuhlii*. However, on every occasion we were struck by the fact that, in a given station (e.g., a small pond, or a portion of several meters along a small stream), we never found more than one such large-headed male, although other males may have been seen there: all other males collected along with the latter had a "normal" or only slightly enlarged head, although some of them were of a size similar to that of the large-headed male of the station. We suggest a possible interpretation for these observations: in each station, a single male might occupy the hierarchical position of a dominant male. This male would develop a very enlarged head but its presence, and most likely also its behaviour (with territorial calls and possibly also fighting with other males) would inhibit the development of enlarged head in all other males nearby. The existence of such an inhibition in dominated males, which could likely be implemented through a hormonal mechanism, could rather easily be submitted to experimental testing, and this could be done by scientists living in countries where these frogs occur.

These observations suggest that, unless large series of specimens are available for study, it is impossible to be sure of the "maximum" development of male sex characters (including the length of the fangs, the width of the head or the size of the cephalic knob) in any species or population of *Limnonectes*. It is therefore advisable to look for other characters to distinguish species, because, when only the development of male sex characters is available in this respect, these characters may be misleading, being in part due to the studied males occupying a dominant or dominated position in the hierarchy of the group. This remark holds particularly true for frogs of the subgenus *Elachyglossa*, that show a very variable development of the cephalic knob (SMITH, 1922*a-b*; BOURRET, 1942). However, despite these remarks, it should be stressed that, even in those males that do not show a "much enlarged head", the head is significantly proportionally wider in males than in females (OHLER & DUBOIS, 1999).

As concerns the species *Lankanectes corrugatus*, very few museum specimens are available for study outside Sri Lanka, and little is known on its variation, including sexual dimorphism in size and other measurements. No detailed measurements of this species were provided in the two books dedicated to the Sri Lankan frogs by local zoologists (KIRTISINGHE, 1957; DUTTA & MANAMENDRA-ARACHCHI, 1996). BOULENGER (1920) provided measurements for 4 specimens in the London museum, including 3 adult males and 1 female. We provide in tab. 1 our measurements of 4 other specimens, 2 males and 2 females, in the Berlin and Paris museums, including the 3 original syntypes of the species. According to this very limited material, no sex dimorphism appears to exist in this species for either the total size or

the size of head, but this sample is much too small to permit definitive statements in this respect. However, given the limited information currently available, this species would appear to differ from *Limnonectes* in not exhibiting sex dimorphism in the size of head.

While the male secondary sex characters discussed above are exceptional in anurans, two other male characters are very widely distributed in many anuran groups, i.e. the presence of nuptial pads (usually covered with a layer of minute spines) on the first finger (and sometimes also on the prepollex, the second and the third fingers) and the presence of vocal sacs with openings on the sides of the mouth floor. The first of these characters is absent both in *Lankanectes* and in all frogs of the tribe Limnonectini of the Dicroglossinae, i.e. the genera *Limnonectes* and *Taylorana*. As for the second character, as mentioned above, so-called "voiceless" frogs of the genus *Limnonectes* can emit loud territorial calls whose function is probably to keep other males at distance. Some at least of them are known to emit also advertisement calls, i.e. calls whose function is to attract females during breeding. Some members of this genus, as currently understood, do have internal vocal sacs, while others lack them. *Lankanectes corrugatus* produces dull advertisement calls that are very striking for anyone who meets these frogs in the field and that can be heard from several meters in the forest habitat (AD, personal observations); they are evoked by DUTTA & MANAMENDRA-ARACHCHI (1996: 82) as "*Urrm*...". The presence of vocal sacs in these frogs, which had been ignored by GÜNTHER (1864) and BOULENGER (1890, 1920), was noted by KIRTISINGHE (1957) and DUTTA & MANAMENDRA-ARACHCHI (1996).

Other characters

Three final characters related to reproduction may briefly be mentioned here. The first one is parental care, listed by EMERSON et al. (2000) in their "definition" of the genus *Limnonectes*. However, according to currently published observations (ALCALA, 1962; INGER, 1966, 1985; INGER et al., 1986; INGER & VORIS, 1988; EMERSON, 1996; INGER & STUEBING, 1997; BROWN & ISKANDAR, 2000), parental care is only known in some species of the *Limnonectes microdiscus* group of the nominative subgenus *Limnonectes* (sensu DUBOIS, 1987*b*) and cannot be included among the characters diagnostic of the whole genus *Limnonectes*, at least as currently understood. According to ISKANDAR (in EMERSON, 1996, see DUBOIS, 1999), a species of this group shows endotrophic development of embryos within the genital tract of the female. In another group of Limnonectini, the genus *Taylorana*, direct development occurs in eggs laid in terrestrial nests (TAYLOR, 1962; OHLER et al., 1999). All these observations confirm the tendency that exists in this group for correlative increase of the size of eggs with reduction of their numbers, leading eventually to direct development or ovoviviparity, a tendency already identified by DUBOIS (1975).

A second interesting character is the position of the arms of the male during amplexus. Although this has never been mentioned in the literature, we observed on various occasions (AD & AO, unpublished observations, briefly mentioned in MARMAYOU et al., 2000: 295) that in the species *Phrynoglossus martensii* Peters, 1867, type-species of *Phrynoglossus* Peters, 1867, amplexus is lumbar, not axillary. This is a strong reason, added to the morphological ones (SMITH, 1931; TAYLOR, 1962; OHLER & DUBOIS, 1999) for considering *Occidozyga* as a genus distinct from *Phrynoglossus*, and not as a synonym of the latter, as suggested by some authors (INGER, 1954, 1966, 1996), or even as a subgenus of *Rana* (EMERSON & BERRIGAN, 1993).

Another peculiarity of *Phrynoglossus* is its unpigmented eggs, that most likely are deposited under some shelter, but, to the best of our knowledge, reproduction and egg-laying has never been described in this genus. The amplectic position of *Lankanectes corrugatus* has never been observed so far (Pethiyagoda, personal communication). As for the eggs, in this species they are pigmented, thus differing from those of *Phrynoglossus*.

Conclusion: taxonomic allocation of the new genus

We presented above in tab. 1 a list of characters that we consider diagnostic of the genera *Euphlyctis*, *Lankanectes*, *Limnonectes*, *Nyctibatrachus*, *Occidozyga*, *Phrynoglossus* and *Taylorana*. All these genera have in common the presence of a forked omosternum, that distinguishes them from the Raninae. However, the phylogenetic data recently provided by several teams (Bossuyt & Milinkovitch, 2000; Vences et al., 2000; Delorme et al., submitted) suggest that these seven genera must be referred to several subclades within the Ranidae, which we taxonomically treat as distinct provisional subfamilial taxa. (1) *Euphlyctis*, *Limnonectes* and *Taylorana* are members of the Dicroglossinae Anderson, 1871; (2) *Occidozyga* and *Phrynoglossus* are members of the Occidozyginae Fei, Ye & Huang, 1991; and (3) *Nyctibatrachus* is a member of the Nyctibatrachinae Blommers-Schlösser, 1993. As for *Lankanectes corrugatus*, the cladistic data available (Bossuyt & Milinkovitch, 2000; Vences et al., 2000; Delorme et al., submitted) suggest not only that it belongs in a genus distinct from *Limnonectes*, but also that it cannot be maintained in the subfamily Dicroglossinae. For the time being, given the data of Bossuyt & Milinkovitch (2000) and Vences et al. (2000), the closest relatives of this genus would appear to be the subfamilies Raninae and Nyctibatrachinae, but both groups exhibit characters widely different from those of *Lankanectes*. From the Raninae, *Lankanectes* differs readily by its forked omosternum and by a completely different general habitus. As for the Nyctibatrachinae, except for the forked omosternum the new genus only shares with *Nyctibatrachus* a few derived characters presumably related to the aquatic mode of life of both genera (general body shape, short legs, short internarial distance), but both genera show significant differences in a number of other characters (extremities of digits, lateral-line system in adults, network of ridges on dorsal parts, femoral glands, fangs and nuptial pads in males, tadpole keratodont formula), which do not support the inclusion of the new genus in the Nyctibatrachinae. The only solution for the time being is to refer the new genus to a new provisional suprageneric taxon, which, as well as all other such taxa, will have to be tested by subsequent works (for more details, see Dubois, 1999).

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APPENDIX 1

COMPARATIVE MATERIAL EXAMINED

Specimens marked with an asterisk (*) are those which were used for the morphometric analyses (tab. 2-3, fig. 2-3)

Euphlyctis cyanophlyctis (Schneider, 1799). – NEPAL. *Dillikot*, 2400 m. MNHN 1975.2164*, 1975.2182*-2183*, 1975.2194*, 1975.2196*; *Samchare*: MNHN 1977.1364-1403; *Sukhet*, 900 m. MNHN 1996.9274-9280; *Tatopani Khola*, 2200 m: MNHN 1975.2250-2273.

Euphlyctis hexadactylus (Lesson, 1834). – INDIA: NMW 2512.1*-5*, 25121*.

Limnonectes (Elachyglossa) doriae (Boulenger, 1887). – MYANMAR: *Mount Carin*, 900-1000m: MNHN 1893.435*-437*.

Limnonectes (Elachyglossa) gyldenstolpei (Andersson, 1916). – LAOS: Ban Tap, Bokeo: MNHN 1997.4149*-4152*. – THAILAND: *Bang Hue Pong, Koon Tan Mountains, Lamphun Province*: NRM 1656*, holotype; *Phu Kradung, Samkokpai, 860-870 m, Loei Province*: MNHN 1987.3132*.

Limnonectes (Elachyglossa) toumanoffi (Bourret, 1941). – CAMBODIA: MNHN 1948.126*, holotype.

Limnonectes (Limnonectes) (gr. grunniens) blythii (Boulenger, 1920). – THAILAND: *Khao Phra Tiu*: MNHN 1986.3154*-3168*.

Limnonectes (Limnonectes) (gr. kuhlii) cf. kuhlii (Tschudi, 1838). – INDONESIA. *Sumatra, Sidikalang*: MV 80*, MV 82*, MV 102*-103*, MV 105*, MV 108*, MV 111*-112*, MV 117*, MV 127*. – THAILAND: *Doi Inthanon*: MNHN 1987.3197. – VIETNAM: *Tonkin*: MNHN 1938.0030.

Limnonectes (Limnonectes) (gr. microdiscus) leytensis (Boettger, 1893). – PHILIPPINES: Dumaguete: MNHN 1964.0283*.

Limnonectes (Limnonectes) (gr. microdiscus) woodworthi (Taylor, 1923). – PHILIPPINES: *Baybay*: MNHN 2000.0611*-0612*.

Nyctibatrachus beddomei Boulenger, 1882. – INDIA: *Tinnevelly*: BMNH 1882.2.10.27-30*, NHMB 1271*.

Nyctibatrachus humayuni Bhaduri & Kripalani, 1955. – INDIA. BMNH 1958.1.4.25*-26*.

Nyctibatrachus deccanensis Dubois, 1984. – INDIA: *Anamallays*: BMNH 1947.2.4.47*, 1947.2.4.49*, 1947.2.4.52*, 1947.2.4.55*, syntypes of *Rana pygmaea* Günther, 1876.

Occidozyga lima (Gravenhorst, 1829). – CAMBODIA: BMNH 1861.4.12.31*-32*. – CHINA. BMNH 1932.5.1.2*, holotype of *Houlema obscura* Gray, 1831. – INDONESIA: *Java*: BMNH 1844.2.22.94A*-94C*. – THAILAND: *Siam*: BMNH 1859.7.1.36*-39*. – CHINA: *Jinghong, Yunnan Province*: MNHN 1999.6416*-6422*.

Phrynoglossus magnapustulosus Taylor & Elbel, 1958. – CHINA: *Jinghong, Yunnan Province*. MNHN 1999.6442-6453.

Phrynoglossus martensii Peters, 1867. – THAILAND. Khao Chong, Trang Province: MNHN 1987.2894*, 1987.2898*, 1987.2907*, 1987.2915*, 1987.2925*, 1987.2934*, 1987.2938*, 1987.2940*, 1987.2958*, 1987.2960*.

Pipa carvalhoi (Miranda-Ribeiro, 1937). – BRAZIL. *Bahia*. MNHN 1981.298-299.

Pseudis paradoxus (Linnaeus, 1758). – VENEZUELA: *Montecal*: MNHN 1983.0390.

Rana (Pelophylax) hubeiensis Fei & Ye, 1982. – CHINA: *Zhejiang*: MNHN 1931.0064-0066.

Silurana tropicalis Gray, 1864. – GUINEA: *Mount Nimba, Region of N...*: MNHN 1944.0162-0164, 1994.1907-1927.

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Systematic review and molecular phylogenetic relationships of the direct developing Malagasy anurans of the *Mantidactylus asper* group (Amphibia, Mantellidae)

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The taxonomy and distribution of Malagasy frogs of the *Mantidactylus asper* group (included in the subgenus *Gephyromantis*) is revised. The group is considered to include *Mantidactylus asper*, *M. spinifer*, *M. luteus*, *M. plicifer*, *M. sculpturatus* (which is resurrected from the synonymy of *M. luteus*) and a new species described herein. Lectotypes are designated for *Rana aspera* Boulenger, 1882 (*Mantidactylus asper*), *Mantidactylus ceratophrys* Ahl, 1929 (junior synonym of *M. asper*) and *Rana plicifera* Boulenger, 1882 (*Mantidactylus plicifer*). *M. asper* and *M. spinifer* are characterized, among other features, by a distinct black-brown contrasted ventral pattern, presence of an outer metatarsal tubercle, and a moderate amount of webbing. They are apparently allopatrically distributed, *M. spinifer* occurring in south-eastern Madagascar and *M. asper* inhabiting eastern and north-eastern rainforests. *M. luteus*, *M. plicifer* and *M. sculpturatus* have a largely uniform light venter, lack the outer metatarsal tubercle and have more extended webbing. A reliable distinction of these three species is only possible in adult males, and is based on differences in femoral gland size and advertisement calls. *M. luteus* is mainly distributed in lowlands along the Malagasy east coast, while *M. sculpturatus* appears to be restricted to mid-altitudes. *M. plicifer* has been found sympatrically with *M. sculpturatus* and *M. luteus*, and is known from the south-east. The new species described herein shares characters with *M. asper* and *M. spinifer* (presence of an outer metatarsal tubercle) and with *M. luteus*, *M. plicifer* and *M. sculpturatus* (uniform venter, extended webbing). It is only known from Montagne d'Ambre in far northern Madagascar.

A molecular phylogenetic analysis based on partial sequences of the mitochondrial 16S rRNA gene supported monophyly of the *M. granulatus* group and of the *M. pseudoasper* group in the subgenus *Phylacomantis*, and of a clade containing *M. luteus*, *M. plicifer* and *M. sculpturatus*. In contrast, the *M. asper* group and the subgenus *Gephyromantis* as a whole appeared to be paraphyletic. The obtained trees indicated a possible evolution of the direct-developing lineage from brook breeding ancestors, and a reversal from direct development in *M. granulatus*. Although these

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aspects received no relevant bootstrap support, they constitute hypotheses of great interest for general questions on amphibian evolution and should be tested with extended data sets.

INTRODUCTION

The Malagasy genus *Mantidactylus* currently contains more than 70 species which show a large diversity in morphology and reproductive biology. DUBOIS (1992) and GLAW & VENCES (1994) divided the genus into a total of 12 subgenera, reflecting this diversity. Major characteristics of all *Mantidactylus* include the absence of nuptial pads in males (and, as far as known, of a strong mating amplexus), and the deposition of eggs outside the water in all species studied so far (BLOMMERS-SCHLÖSSER, 1979). Most species additionally have specialized femoral glands on the ventral surface of thighs (GLAW et al., 2000), especially in males.

GLAW & VENCES (1994) distinguished three major clades within *Mantidactylus*. One group contains more or less arboreal species which mostly deposit their eggs on leaves above the water surface; their tadpoles are rather generalized (subgenera *Blommersia*, *Guibemantis*, *Pandanusicola*, *Spinomantis*). A second group consists of brook-edge-dwelling species, the larvae of which often show specialized mouthparts (subgenera *Brygoomantis*, *Chonomantis*, *Hylobatrachus*, *Mantidactylus*, *Ochthomantis*). The third assemblage contains three subgenera (*Gephyromantis*, *Laurentomantis*, *Phylacomantis*). while *Phylacomantis* males usually call along brooks and at least some species have free-swimming larval stages, calling males of most *Laurentomantis* and *Gephyromantis* do not aggregate around water bodies, and direct development without free-swimming larval stages has been demonstrated in two species, *Mantidactylus asper* and *M. eiselti* (BLOMMERS-SCHLÖSSER, 1979; GLAW & VENCES, 1994). Due to this reproductive diversity, studies on these frogs have the potential to contribute to the understanding of the evolution of direct development and other specializations in anuran reproductive biology.

One basic pre-requisite for such studies, however, is a detailed basic knowledge on the species' taxonomy and distribution (GLAW & VENCES, 2000). Distributional data of Malagasy frogs are largely based on the monograph of BLOMMERS-SCHLÖSSER & BLANC (1991) who, however, mostly did not recognize sibling species and gave no voucher specimens for the localities plotted on their distribution maps. Apart from type specimens from other collections, their work was based almost exclusively on the collections housed at Amsterdam and Paris.

In the present paper, we review the *Mantidactylus asper* group, a phenetic species assemblage in the subgenus *Gephyromantis*, distinguished from other *Mantidactylus* by reproduction independent from water, mainly nocturnal calling behaviour, largely separated lateral metatarsalia, and black paired subgular vocal sacs in males. We re-examined the material available to BLOMMERS-SCHLÖSSER & BLANC (1991), and complemented this information by own field observations.

MATERIALS AND METHODS

ABBREVIATIONS AND MEASUREMENTS

Vocalizations were recorded using portable tape recorders with an external microphone (Vivanco EM 238) and were analyzed with the MEDAV sound analyzing system Spektro 3.2. The following morphological measurements were taken with a caliper to the nearest 0.1 millimeter: SVL, snout-vent length; HW, head width; HL, head length, ED, horizontal eye diameter; END, eye-nostril distance; NSD, nostril-snout tip distance; NND, nostril-nostril distance; TD, horizontal tympanum diameter; HAL, hand length; FORL, forelimb length; HIL, hindlimb length; FOL, foot length, FOTL, foot length including tarsus, IMTL and IMTH, length and height of inner metatarsal tubercle; TL1, length of first toe. Statistical analyses were carried out using SPSS for Windows, version 10. We performed Mann-Whitney *U* tests to test significance of intersexual differences in size and morphometric ratios (TD/SVL, relative tympanum diameter; IMTL/SVL and IMTH/SVL, relative size of inner metatarsal tubercle, FORL/SVL and HIL/SVL, relative length of fore- and hindlimbs), and of interspecific differences in selected morphological variables and ratios. Measurements are given as range, with mean ± standard deviation in parentheses.

INSTITUTIONAL ABBREVIATIONS

BMNH, The Natural History Museum, London (formerly British Museum of Natural History); MNHN, Muséum National d'Histoire Naturelle, Paris, MRSN, Museo Regionale di Scienze Naturali, Torino, MSNG, Museo Civico "G. Doria" di Storia Naturale, Genova; MTKD, Museum für Tierkunde, Dresden; TM, Transvaal Museum, Pretoria; UADBA, Université d'Antananarivo, Département de Biologie Animale, ZFMK, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, ZMA, Zoölogisch Museum, Amsterdam, ZMB, Museum für Naturkunde, Berlin; ZSM, Zoologische Staatssammlung, München. The catalogue numbers of voucher specimens housed in the ZMA are given as the jar number followed by the field number of R. Blommers-Schlösser, since they bear no individual ZMA tags.

TAXONOMY

To avoid confusion by introducing working definitions (operational taxonomic units) and assigning them to specific names in a second step, we decided to anticipate our taxonomic proposals and use consistent names throughout this paper. This mainly regards (1) the recognition of the Montagne d'Ambre population previously considered as *Mantidactylus plicifer* by BLOMMERS-SCHLÖSSER & BLANC (1991) or as *M.* cf. *asper* by GLAW & VENCES (1994) as a new species which is described herein, (2) the re-definition of *Mantidactylus plicifer* as a

species of usually rather large body size and with large and distinct femoral glands from south-eastern Madagascar; (3) the recognition of mid-altitude eastern populations previously assigned to *M. luteus* by GLAW & VENCES (1994) as a distinct species *M. sculpturatus*. These decisions are largely corroborated by high genetic divergence levels between the species recognized, by the morphological differentiation of the new species from Montagne d'Ambre and by the morphological and bioacoustic differentiation and syntopic occurrence of *M. sculpturatus* and *M. plicifer* at Ranomafana. More detailed justifications are given in the respective *Identity* and *Diagnosis* sections below.

MORPHOLOGICAL TERMINOLOGY

Webbing formula is given according to BLOMMERS-SCHLÖSSER (1979). Femoral gland morphology is described according to GLAW et al. (2000). Most *Gephyromantis* species are characterized by a number of dermal spines, tubercles and ridges. The arrangement and degree of expression of these structures is often important for species definitions and probably also bears relevance for the assessment of phylogenetic relationships among species and subgenera in the genus *Mantidactylus*. To refer unequivocally to these structures, we here define a number of terms (fig. 1):

(1) *Inter-ocular tubercles*. – On the upper surface of the head, between the eyes, a number of tubercles are present in many species. These are generally arranged symmetrically, either as one pair or as two pairs, and should not be mistaken with the unelevated black inter-ocular spots as present in *M. leucomaculatus* (*Phylacomantis*). In several *Phylacomantis* (*M. cornutus*, *M. redimitus*, *M. tandroka*, *M. tschenki*), one pair of rounded, black tubercles are generally present. On the contrary, in *M. asper*, *M. spinifer* and the new species described herein (*Gephyromantis*), the tubercles are generally not rounded but rather longitudinal and ridge-like; often, two pairs of such tubercles are present which sometimes appear to be a discontinuous anterior continuation of the inner dorsolateral ridges, and sometimes, in *M. spinifer*, these ridge-like tubercles are fused to form a symmetrical figure (fig. 1).

(2) *Inner dorsolateral ridges*. – As a constant state in all species of the *M. asper* group, two largely continuous ridges start above or up to 4 mm behind the eyes and run medially onto the anterior back. Here they either continue straight dorsolaterally onto the posterior fourth of the back, or curve slightly towards the flanks and fade.

(3) *Outer dorsolateral ridges*. – In all species of the *M. asper* group, a second pair of dorsolateral ridges runs laterally of the inner dorsolateral ridges. Often this second pair is not continuous and poorly defined.

(4) *Connecting dorsal ridge*. – In some *M. spinifer*, at the point of maximum convergence of the inner dorsolateral ridges on the anterior dorsum, these are connected by a short transversal ridge.

(5) *Supraocular spines*. – Above the eyes, distinct dermal spines are usually present in all species of the *M. asper* group (and in several *Phylacomantis*: e.g., *M. cornutus*, *M. redimitus*, *M. tschenki*), although they can be small and indistinct in the new species described herein. In contrast to the rather rigid dorsal ridges, these spines are flexible.

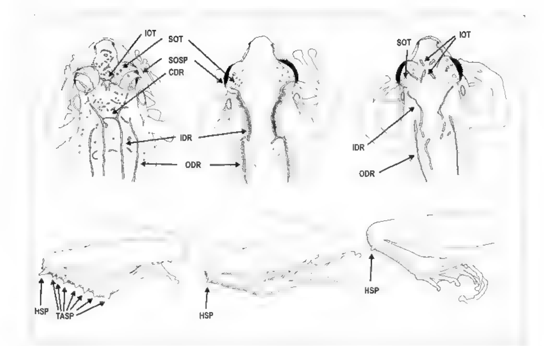


Fig. 1. - Partial dorsal views (head and anterior body and hindlimb) of three representative species of the *Mantidactylus asper* group. *Mantidactylus spinifer* (left), female MNHN 1972.1444, *M. plicifer* (center), female MNHN 1972.1431, and *M. ambohitra* (right), female MNHN 1893.245. The arrows mark dermal structures which are described in the text. CDR, connecting dorsal ridge, HSP, heel spine, IDR, inner dorsolateral ridge, IOT, inter-ocular tubercles, ODR, outer dorsolateral ridge, SOSP, suprocular spines, SOT, supraocular tubercles. TASP, tarsal spines. Not to scale.

(6) *Supraocular tubercles*. These are homologous to supraocular spines but less elevated and not pointed.

(7) *Heel spine*. A long or short spine may be present on the heel. Similar to the supraocular spines, the heel spine is a dermal, flexible structure. Beside the *M. asper* group, it is also found in several *Phylacomantis* and in species of the genus *Boophis* (e.g., *B. madagascariensis*).

(8) *Tarsal spines*. A number of smaller dermal spines are sometimes arranged at the posterior edge of tarsus. Species with tarsal spines always bear also a distinct heel spine.

(9) *Humeral protuberance*. A well known synapomorphy of *Mantidactylus* species are the femoral glands on the ventral surface of the femur (GLAW et al., 2000). In several species of the *M. asper* group (*M. luteus*, *M. plicifer*, *M. spinifer*), we observed a prominent structure on the ventral side of the humerus, too (fig. 2). By dissection (internal view, GLAW et al., 2000), we noted that this prominence was not caused by enlargement of skeletal or muscular tissues but largely dermal, and sometimes contained a gland-like element at its most prominent part. Without further histological analyses we are unable to state whether this structure is actually a gland, and thus here refer to it as humeral protuberance. It is best visible in



Fig. 2. – Left: ventral views of a male (above; MNHN 1972.1462) and a female (below; MNHN 1972.1443) of the forelimb of *Mantidactylus spinifer*. The arrows mark the humeral protuberances. Note also the strongly contrasted ventral pattern in both sexes. Right: ventral views of a male (above: MNHN 1972.1436) and a female (below: MNHN 1972.1431) of the forelimb of *M. plicifer*. In this species, the humeral protuberance is very distinct in males but apparently absent in females.

Mantidactylus plicifer and *M. luteus*, where a clear sexual dimorphism exists (no protuberance recognizable in females; fig. 2). In other species, e.g. *M. spinifer*, a weakly expressed humeral protuberance appears to be present in males and females (fig. 2).

Molecular and phylogenetic methods

To sample data on genetic differentiation and phylogenetic relationships, we sequenced fragments of the mitochondrial 16S rRNA gene of up to 567 base pairs (bp), using primers and protocols given by Vences et al. (2000), in species of the *M. asper* group and of related taxa. The corresponding voucher specimens and EMBL/Genbank accession numbers are: *Mantidactylus asper*, UADBA-FG/MV 2000.17, AJ314802; *M. luteus*, ZFMK 66674, AF215313; *M. plicifer*, ZFMK 62306, AJ314800; *M. sculpturatus*, ZFMK 62304, AJ314799; *M. boulengeri*, ZFMK 66672, AF215318; *M. corvus*, ZFMK 70494, AF215320; *M.* cf. *pseudoasper*, MSNG 49087, AJ314803; *M. malagasius*, MRSN A1991, AJ314797; *M.* aff. *malagasius*, MRSN A1938, AJ314796; *M. granulatus*, ZSM 645.2001, AJ314794; *M.* sp. n. (Tsaratanana; new species close to *M. granulatus*), ZSM 627.2001, AJ314795; *M. leucomaculatus*, ZFMK 59953, AJ314805; *M. cornutus*, ZSM 308.2000, AJ314798; *M. tschenki*, ZFMK 62296, AJ314806; *M. tandroka*, ZFMK 59894, AJ314803. *Boophis xerophilus* (ZFMK 66705,

AF215335) and *Mantidactylus liber* (subgenus *Guibemantis*; ZSM 491.2000, AJ314801) were used as outgroups. Sequences of the new species described below were obtained from the specimen MTKD 37424 and have the Genbank accession number AF215327.

Sequences were aligned using the CLUSTAL algorithm in SEQUENCE NAVIGATOR (Applied Biosystems); subsequently, the alignment was adjusted by eye. A total of 33 base pairs of the hypervariable region could not be reliably aligned and were excluded from further analysis. The aligned sequences were submitted to analysis using PAUP*, version 4.0 (SWOFFORD, 2001). We used MODELTEST (POSADA & CRANDALL, 1998) to estimate the model of sequence evolution for a Maximum Likelihood (ML) phylogenetic reconstruction. We additionally performed Maximum Parsimony (MP) analyses, using the heuristic search option with tree-bisection reconnection branch-swapping, and Neighbor-joining (NJ) analyses, with LogDet distances which are robust against possible variation of sequence evolution among lineages (LOCKHART et al., 1994). In the MP analyses, we coded gaps as fifth state, but also performed additional searches excluding all characters with gaps in one or more species. We used PAUP* to test for the presence of a significant phylogenetic signal by a permutation-tailed-probability (PTP) test with 100 replicates, and for homogeneity of base frequencies across sequences.

RESULTS

SPECIES ACCOUNTS

Mantidactylus asper (Boulenger, 1882)

(fig. 3a-b)

Rana aspera Boulenger, 1882 – *Name bearing type*: lectotype, by present designation, BMNH 1882.3.16.80, adult male collected by W. D. Cowan, SVL 27.8 mm. *Type locality*: "East Betsileo" according to original description. *Other types*: paralectotypes, following present lectotype designation, BMNH 1882.3.16.81-90, same collecting data as lectotype.

Mantidactylus ceratophrys Ahl, 1929 – *Name bearing type*: lectotype, by present designation, ZMB 10443, adult female, collected by J. M. Hildebrandt according to original description. *Type locality*: "Betsileo" according to original description. *Other types*: paralectotypes, following present lectotype designation, ZMB 10444 and 50501-50502, three adult females with same collecting data as lectotype.

Comments. (1) Considering the existence of at least one new species in the *M. asper* group as described below it appears important for taxonomic stability to define single name-bearing types for all taxa in the group. Following this rationale, we here designate lectotypes for *M. asper* and its junior synonym *M. ceratophrys*. Detailed morphological measurements of these lectotypes are given in tab. 1. (2) BLOMMERS-SCHLOSSER & BLANC (1991) listed the specimens "BMNH 1882.316.80-82, 83-86" as syntypes of *M. asper*. The number "316" in this mention is certainly a typing error for "3.16". Beside BMNH 1882.3.16.80-81, all specimens of the



Fig. 3. – Photographs of *Mantidactylus asper*, male from Ankeniheny (ZFMK 60789) in dorsolateral and ventral views (a-b), of *Mantidactylus ambohitra* male holotype from Montagne d'Ambre (ZSM 1084/2001) in dorsolateral and ventral views (c-d), and of two additional specimens of *M. ambohitra*: female ZFMK 57419 (e) and a calling male specimen (not collected), photographed by J. Köhler (f), both from Montagne d'Ambre.

series BMNH 1882.3.16.83-90 are labeled as syntypes of the taxon in the London museum. We examined four specimens of this series which were not individually numbered. We could not locate the specimen BMNH 1882.3.16.82 in the London collection; it may have been exchanged or used for osteological examinations. It can be assumed that the series of paralectotypes (according to present lectotype designation) consists of at least nine, possibly ten specimens. – (3) Blommers-Schlösser & Blanc (1991) stated that the type of *Mantidac*

tylus ceratophrys Ahl, 1929 was lost In the meantime, four original syntype specimens have been rediscovered in the ZMB collection (lectotype and paralectotypes according to present designation).

Material examined. BMNH 1882 3 16 80-81, 1882 3 16 83-86 (East Betsileo, lectotype and paralectotypes), BMNH 1925 7 2 29 (Antsihanaka), BMNH 1928 5 9 1 (Brickaville), MNHN 1972 557-558 (Tsaratanana), MNHN 1972 559-560 (Mandraka), MNHN 1972 574-576, 1972 578-583, 1972.586-591 (Tsaratanana); MNHN 1972 584-585 (locality uncertain), MNHN 1973 905 (Marojejy, alt 1300 m), MNHN 1975 313 (Marojejy), MNHN 1975.317 (no precise locality), MNHN 1975.318 (Marojejy, alt 1300 m), MNHN 1975 319-320 (Marojejy, alt 2000 m), MNHN 1975 321 (Mandraka); ZFMK 62236-62237, 62240 (Mantady), ZFMK 62303 (Ranomafana); ZFMK 60789 (Ankeniheny), ZMA 6867 988-990 and 6868 470 (Andasibe), ZMA 6894 36, 6895 376-383 and 6895.480-482 (Mandraka), ZMA 6897 906 (Andasibe); ZMB 50501-50502 and 10443-10444 (Betsileo, lectotype and paralectotypes of *Mantidactylus ceratophrys*); ZSM 401 2000 and UADBA-FG/MV 2000.17 (Mandraka).

Morphology and diagnosis. The following morphological description is based on the type series, and on specimens from central eastern Madagascar (Mandraka, Andasibe, Mantady, Antsihanaka, Brickaville). Specimens from these localities form a well-defined homogeneous cluster, although several characters (expression of dorsal tubercles and ridges, relative hindlimb length) are subject to considerable individual variation. Other attributed specimens are discussed in the section on distribution.

Inner dorsolateral ridges prominent, either continuous (e.g in ZMA 6867.990) or discontinuous (e g in ZMA 6867.989), starting 1-3 mm behind eyes. No connecting dorsal ridge in the specimens examined by us. Outer dorsolateral ridges generally present, but often not continuous, appearing as an irregular series of short folds and tubercles. One or two pairs of distinct more or less prominent ridge-like interocular tubercles. Additional smaller tubercles and short ridges on the dorsum of most specimens. Distinct supraocular spines in all specimens, two of these being especially large A distinct heel spine; tarsal spines generally reduced to small tubercles, sometimes not recognizable (e g. in several specimens of the type series). Femoral glands usually visible in males, but not very distinct or prominent. Vocal sac paired subgular No clearly recognizable humeral protuberance in either sex Webbing in most specimens reaching slightly beyond the first subarticular tubercle of the fifth toe; webbing formula 5(0.5) to 5(0.75) One inner and two outer metacarpal tubercles, the latter in contact with each other. A large (males) or medium-sized (females) inner metatarsal tubercle and a distinct, small to medium-sized outer metatarsal tubercle.

Significant or near-significant intersexual differences were found in SVL (Mann-Whitney *U* test, $P < 0.06$), in relative length of the inner metatarsal tubercle ($P < 0.005$), and in relative tympanum diameter ($P < 0.05$), but not in relative height of the inner metatarsal tubercle or limb length Males had larger relative tympanum sizes and longer inner metatarsal tubercles than females. Male/female size ratio was 97 %.

Coloration. In preservative, dorsal coloration generally brown, with more or less symmetrical light brown or dark brown markings. In ZMA 6867 988, dark brown vertebral area enclosed between inner (anterior dorsum) and outer (posterior dorsum) dorsolateral ridges, and beige flanks and areas lateral to the ridges, the beige color starting as narrow dorsolateral bands above the eyes. Hindlimbs brown with dark brown crossbands. A thin light vertebral line in ZFMK 62236. Head laterally brown, including the lips, with some rather indistinct

dark brown markings. Ventral side white on the chest and, in females, on the throat, more cream on the posterior belly. Throat in males light brown with a distinct central white longitudinal stripe, and with black lateral color coinciding with the inflatable parts of the vocal sac. In females, indistinct but sharply delimited brown vermiculations on throat and chest. Limbs ventrally light brown, with some darker pattern at the edges.

Distribution. – Beside the specimens from central eastern Madagascar, we also assign to *M. asper* rather than to *M. spinifer* one subadult male from Ranomafana (ZFMK 62303; vocal sac not visible, but throat laterally already slightly black colored) based on its smaller size, ventral pattern, and expression of ridges and tubercles. The situation is more difficult for the available material from the Marojejy and Tsaratanana massifs in northern Madagascar. These specimens are larger than typical *M. asper*, have more weakly expressed spines and ridges (supraocular spines reduced to tubercles in most specimens), and a very weak ventral pattern. In part, they thus remind specimens from Montagne d'Ambre which are described below as a new species. However, the low amount of webbing (at fifth toe consistently 0.75-1), as well as other characters constitute a distinct difference to that species, and support the tentative inclusion of the Tsaratanana and Marojejy populations in *M. asper*. Despite low number of females in this sample (only two specimens), the inner metatarsal tubercle is significantly relatively longer in males ($P < 0.05$, tab. 2-3). Male/female size ratio is 99 %.

Summarizing, the species is known from the following precise localities: (1) Tsaratanana; (2) Marojejy; (3) Antsihanaka, (4) Brickaville; (5) Mantady; (6) Andasibe, (7) Ankeniheny; (8) Mandraka; (9) Ranomafana. Except for Brickaville, which is located close to sea level at the east coast, all localities in the central east are at mid-elevations, ranging from ca. 700 to 1200 m. Marojejy specimens are catalogued as originating from an elevational range of 1300-2000 m.

Blommers-Schlösser & Blanc (1991) additionally recorded the species from Les Roussettes (Montagne d'Ambre) and Ambatofitoharanana. Specimens from the former locality are here attributed to the new species described below, while the voucher specimen from Ambatofitoharanana (MNHN 1975 315) cannot be reliably attributed to any described species (see section at the end of the species accounts).

Natural history. – Calling males were observed during the day on the ground (at Ankeniheny) and after dusk from branches about 50 cm above the ground (at Mantady and Mandraka). At Ankeniheny, they were mainly found close to a swampy brook, while they called far from water bodies at Mantady, and close to a tiny brook at Mandraka. Vocal sacs did not remain inflated between notes. Each note was one expiration.

Advertisement call. – Calls were recorded at Ankeniheny on 18 February 1994, 17:15 h, at 23.5°C air temperature. They consisted of series of single notes or series of note groups of 2-4 notes each (fig. 4). Note duration was 5-13 ms (10 ± 3 ms, $n = 8$), duration of intervals between notes was 56-80 ms (66 ± 11 ms, $n = 6$). Frequency was 1700-7700 Hz, dominant frequency 3200-4200 Hz.

Similar calls were heard after dusk on 10 February 1996 at Mantady. Only series of single notes were heard (note repetition rate 1.3-1.4 per second). Frequency was about 2000-5000 Hz, dominant frequency 3500-4500 Hz.

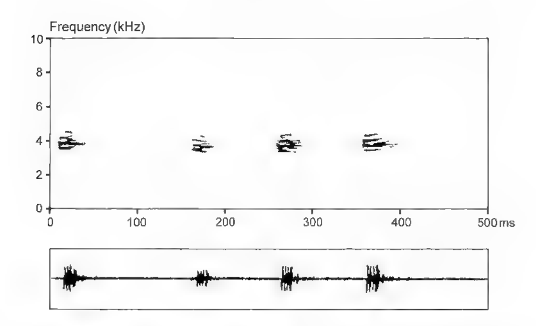


Fig. 4. – Sonagram and oscillogram of a call (series of four notes) of *Mantidactylus asper* from Ankenіheny.

Calls from Mandraka (recorded by R. Blommers-Schlösser in December 1972 at 17.00 h) were series of note groups (up to 7 notes per group). Note duration was 13-20 ms (16 ± 2 ms, n = 9), duration of intervals between notes 72-80 ms (75 ± 2 ms, n = 7). Note groups with 4-7 notes had a duration of 323-494 ms (386 ± 69 ms, n = 5), duration of intervals between note groups was 626-733 ms (684 ± 44 ms, n = 4). Frequency was 1800-6000 Hz without recognizable dominant frequency.

Mantidactylus spinifer Blommers-Schlösser & Blanc, 1991

Mantidactylus spiniferus Blommers-Schlösser & Blanc, 1991. – *Name-bearing type*: holotype, by original designation, MNHN 1972.1450, adult male collected by C. P. Blanc in November-December 1971 according to MNHN catalogue. - *Type locality*: "Chaines Anosyennes" according to original description, "Camp IV, Chaines Anosyennes" according to MNHN catalogue. - *Paratypes*: MNHN 1972.1440 and 1972.1470, adult female and male.

Material examined. – (1) types and topotypical material: MNHN 1972.1450 (holotype, Camp IV, Chaînes Anosyennes), MNHN 1972.1440 (paratype, Camp IV, Chaînes Anosyennes), MNHN 1972.1470 (paratype, Ambana-Camp IV, Chaînes Anosyennes), MNHN 1972.1439, 1972.1443-1468 (Camp IV, Chaînes Anosyennes); (2) further material: MNHN 1972.551-554 (Ivohibe, Marovitsika forest).

Morphology and diagnosis. – Beside the three type specimens designated by BLOMMERS-SCHLÖSSER & BLANC (1991), nine males, thirteen females and four juveniles from the same

series and general locality were available. Considering this material, the following updated description of *M. spinifer* (based on the topotypic material only) can be provided. Identity of other specimens is discussed in the section on distribution.

Inner dorsolateral ridges prominent, starting 0-2 mm behind the eye. Dorsal connecting ridge present in some specimens and completely absent in others. Outer dorsolateral ridges generally present, but mostly not continuous and poorly defined, often appearing as an irregular series of short folds and tubercles. One pair of distinct and very prominent ridge-like interocular tubercles, a second, less distinct anterior pair often being also visible, the two pairs sometimes fusing to a single symmetrical structure (fig. 1). A large number of additional irregular tubercles and short ridges scattered on the dorsum. Distinct supraocular spines in all specimens, two of these being especially large. A distinct heel spine and a line of 2-7 distinct tarsal spines. Males with very distinct and rather prominent femoral glands. Vocal sac paired subgular. A weakly expressed humeral protuberance in both sexes (fig. 2). Webbing in most specimens reaching distinctly beyond last subarticular tubercle of fifth toe, but not reaching toe disc. webbing formula 5(0.25) to 5(0.75). One inner and two outer metacarpal tubercles, the latter two in contact with each other. A large inner and a distinct, small to medium sized outer metatarsal tubercle.

Morphometric measurements are given in tab. 1-3. No significant sexual dimorphism was found in relative forelimb length ($P > 0.5$), but the remaining variables tested showed significant differences between sexes: females were significantly larger (mean male/female size ratio 96 %, $P < 0.05$), had shorter relative hindlimbs ($P < 0.05$), and smaller relative tympanum sizes ($P < 0.01$). Relative length and height of the inner metatarsal tubercle were also distinctly smaller in females ($P < 0.001$).

Coloration. - The following description is based on preserved specimens only, as no color pictures of living specimens were available. Dorsal coloration with various tones of brown, generally arranged in longitudinal patterns. Narrow or broad brown bands sometimes arranged dorsolaterally, following the dermal ridges, on a beige or light brown dorsum (MNHN 1972.1443, 1972.1449), or dark brown central dorsum with cream-beige flanks (MNHN 1972.1458, 1972.1461). In most specimens a rather indistinct mixture of dark and light brown.

All specimens ventrally with a very distinct coloration, the dark flank color reaching onto the posterior venter and ending abruptly, without any fading, bordering onto the ventral color which (in preservative) is bright white (fig. 2). Males with a brownish throat (laterally black, corresponding to the inflatable parts of the vocal sac) with a more or less distinct median white stripe. Females with a white throat and a brown border along the lower lip. Limbs ventrally more or less distinctly marbled with dark brown and white. This conspicuous ventral color pattern is already visible in juveniles (MNHN 1972.1452, 1972.1466-1468) of 14-18 mm SVL.

Distribution. - Beside the specimens from the type locality Chaînes Anosyennes, BLOMMERS-SCHLÖSSER & BLANC (1991) included three additional localities of *M. spinifer* in their distribution map: Marojejy, Marovitsika and Andringitra. The MNHN vouchers from Marojejy were herein assigned to *M. asper* and we did not locate vouchers from Andringitra assignable to the species. However, a series from the Marovitsika forest (Pic d'Ivohibe) could be included

Table 1. Morphometric measurements (all in mm) of name-bearing types in the *Mantidactylus asper* group. For abbreviations of measured variables, see *Materials and methods*, other abbreviations used are: M (male), F (female). RHL (relative hindlimb length) gives the position reached by the tibiotarsal articulation when the hindlimb is adpressed along the body).

Taxon	*Rana aspera* Boulenger 1882	*Mantidactylus ceratophrys* Ahl, 1929	*Mantidactylus spinifer* Blommers-Schlösser & Blanc, 1991	*Mantidactylus ambohitra* n. sp.	*Rana plicifera* Boulenger, 1882	*Mantidactylus sculpturatus* Ahl, 1929
Status	Lectotype	Lectotype	Holotype	Holotype	Lectotype	Holotype
Number	BMNH 1882 3 16.80	ZMB 10443	MNHN 1972 1450	ZSM 1084 2001	BMNH 1882 3 16 58	ZMB 305 5
Sex	M	F	M	M	M	F
SVL	27.3	30	35.1	35.8	38.8	37.5
HW	9.2	9.2	12.2	13.5	13.1	13.8
HL	10.4	10.7	13.2	13.8	3.7	15
TD	2.4	2.4	2.6	3.1	2.7	2.6
ED	3.6	3.7	4.2	4.6	4.7	5.0
END	2.9	3.2	3.4	3.3	3.4	3.4
NSD	9	2.0	2.3	2.0	2.4	2.2
NND	2.5	2.8	2.7	2.9	4.0	3.7
FORL	17.7	9.2	22.8	22.8	22.5	23.6
HAL	8.8	9.0	1.3	1.1	0	1.8
HIL	5 8	54.3	68.8	69.8	68.3	74.2
FOTL	23.3	25.4	29.4	29.9	30.0	33.0
FOL	15.4	16.3	20.2	21.3	19.5	2 8
IMTL	3	1.3	1.7	1.5	9	4
IMTW	1.0	0.9	1.1	0.9	4	0.8
TLI	2.3	3.2	3.8	4.1	3.4	-
FGL			5.5	-	8.1	-
FGW			2.2	-	3.5	-
RHL	beyond snout tip	nostril	widely beyond snout tip	widely beyond snout tip	beyond snout tip	beyond snout tip

Table 2. Morphometric measurements (all in mm) of male specimens of species in the *Mantidactylus asper* group. Abbreviations as given in *Materials and methods* and in caption to tab. 1. The measurements of *M. asper* are given separately for populations from north-eastern (NE, Tsaratanana, Marojejy) and central eastern (CE) Madagascar. *n* is the number of measured specimens. Measurements are given as mean ± standard deviation (range in parentheses). Relative hindlimb length (RHL) is coded as follows: when adpressed along body, the tibiotarsal articulation reaches (1) the nostril, (2) the snout tip, (3) beyond the snout tip or (4) widely beyond the snout tip.

Species	*M. asper* (CE)	*M. asper* (NE)	*M. spinifer*	*M. ambohitra*	*M. luteus*	*M. plicifer*	*M. sculpturatus*
n	14	19	11	5	12	12	4
SVL	28.3 ± 0.9 (26.6-30.2)	32.8 ± 1.6 (30.8-35.5)	34.1 ± 1.0 (32.5-35.4)	35.9 ± 1.2 (34.0-37.2)	39.0 ± 2.2 (35.7-42.6)	45.0 ± 2.5 (38.8-48.3)	40.3 ± 2.4 (37.9-43.0)
HW	9.3 ± 0.4 (8.7-10.0)	11.9 ± 0.6 (10.9-13.3)	11.5 ± 0.5 (11.0-12.5)	12.7 ± 0.7 (11.5-13.5)	14.1 ± 0.7 (12.2-15.2)	16.4 ± 1.1 (13.1-17.4)	14.7 ± 0.6 (14.0-15.4)
HL	10.6 ± 0.4 (9.9-11.4)	12.8 ± 0.6 (11.7-13.7)	12.9 ± 0.5 (12.2-13.9)	13.4 ± 0.4 (12.8-13.8)	16.0 ± 0.7 (14.6-17.1)	17.7 ± 1.4 (13.7-19.)	16.3 ± 1.2 (14.6-17.2)
TD	2.3 ± 0.3 (2.0-2.8)	2.9 ± 0.3 (2.4-3.3)	2.7 ± 0.1 (2.5-2.9)	2.7 ± 0.3 (2.4-3.1)	2.8 ± 0.2 (2.5-3.1)	2.7 ± 0.2 (2.4-2.9)	3.2 ± 0.3 (2.7-3.5)
ED	3.4 ± 0.2 (3.0-3.7)	3.8 ± 0.2 (3.3-4.)	4.0 ± 0.2 (3.8-4.3)	4.2 ± 0.4 (3.6-4.6)	4.8 ± 0.3 (4.4-5.2)	5.2 ± 0.3 (4.7-5.6)	5.0 ± 0.3 (4.6-5.3)
END	3.0 ± 0.2 (2.6-3.3)	3.4 ± 0.2 (3.1-3.6)	3.5 ± 0.2 (3.2-4.0)	3.3 ± 0.3 (2.9-3.7)	4.2 ± 0.3 (3.7-4.6)	4.5 ± 0.4 (3.4-4.9)	4.5 ± 0.2 (4.3-4.7)
NSD	1.8 ± 0.2 (1.5-2.2)	2.2 ± 0.2 (1.8-2.6)	2.4 ± 0.2 (2.2-2.6)	2 ± 0.2 (2.0-2.4)	2.4 ± 0.2 (2.0-2.7)	3.0 ± 0.3 (2.4-3.5)	2.6 ± 0.3 (2.4-3.0)
NND	2.3 ± 0.2 (1.8-2.5)	2.7 ± 0.3 (2.0-3.2)	2.5 ± 0.2 (2.3-2.7)	2.9 ± 0.3 (2.7-3.4)	3.4 ± 0.3 (2.7-3.8)	4.4 ± 0.2 (4.0-4.7)	3.8 ± 0. (3.7-3.8)
FORL	18.8 ± 1.3 (16.8-21.8)	23.1 ± 1.3 (20. -25.1)	23.2 ± 1.3 (20.9-25.5)	23.8 ± 0.9 (22.7-24.6)	24.8 ± 1.0 (23.3-26.6)	27.9 ± 2.3 (22.5-31.0)	25.4 ± 1.3 (24.4-27.2)
HAL	8.9 ± 0.5 (8.0-9.7)	10.7 ± 0.6 (9.5- 1.8)	1 ± 0.6 (10.1-12.4)	11.2 ± 0.4 (10.7-11.8)	11.5 ± 0.5 (10.4-12.2)	13.5 ± 0.9 (11.0-14.7)	11.9 ± 0.6 (11.3-12.4)
HIL	53. ± 2.4 (49.2-57.7)	63.9 ± 3. (58.1-69.9)	66.1 ± 3.8 (57.0-71.8)	68.2 ± 2. (65.0-70.0)	73.6 ± 4. (66.5-80.1)	85.8 ± 5.9 (68.3-91.0)	79.9 ± 3.2 (77.0-84.3)
FOTL	23.1 ± 1.1 (21.2-25.1)	28.3 ± 1.2 (26.3-30.5)	28.6 ± 1.3 (26.2-30.9)	29.3 ± 0.9 (28.0-30.0)	32.4 ± 1.8 (29.6-35.2)	37.8 ± 2.8 (30.0-40.7)	35.3 ± 1.9 (33.6-38.0)
FOL	15.6 ± 0.6 (14.5-16.8)	19.3 ± (17.8-21.6)	19.2 ± 1.1 (17.4-20.9)	20.4 ± 0.9 (19.1-21.3)	21.4 ± 1.2 (9.2-23.7)	24.7 ± 1.8 (9.5-26.5)	23.3 ± 1.3 (22.4-25.1)
IMTL	1.3 ± 0.2 (1.1-1.7)	1.6 ± 0.2 (1.4-2.0)	1.8 ± 0.2 (1.3-2.1)	1.5 ± 0.1 (1.4-1.7)	1.8 ± 0.3 (1.5-2.3)	2.3 ± 0.2 (1.9-2.6)	1.8 ± 0.1 (1.7-2.0)
IMTW	0.8 ± 0.2 (0.5-1.1)	1.0 ± 0.2 (0.5-1.5)	1.1 ± 0.1 (1.0-1.4)	1.1 ± 0.1 (0.9-1.2)	1.1 ± 0.1 (0.9-1.3)	1.4 ± 0.2 (1.0-1.6)	1.1 ± 0.1 (1.0-1.2)
TLI	2.8 ± 0.3 (2.3-3.2)	3.7 ± 0.4 (3.2-4.6)	3.7 ± 0.3 (3.2-4.2)	4.0 ± 0.2 (3.7-4.2)	4.2 ± 0.4 (3.5-5.0)	5.1 ± 0.6 (3.4-5.8)	4.6 ± 0.4 (4.1-5.0)
FGL	5.0 ± 0.9 (4.2-6.0)	4.9 ± 0.6 (4.5-5.7)	5.5 ± 0.4 (5.0-6.5)	5.1 ± 0.8 (4.5-5.6)	5.9 ± 0.8 (4.6-7.3)	8.4 ± 0.7 (7.5-9.9)	7.0 (*n* = 1)
FGW	1.8 ± 0.3 (.6-2.2)	1.8 ± 0.2 (1.6-2.0)	2.3 ± 0.3 (1.8-2.9)	2.1 ± 0.6 (.7-2.5)	1.6 ± 0.3 (1.3-2.0)	3.2 ± 0.3 (2.5-3.7)	1.6 (*n* = 1)
RHL	1-4	3-4	3-4	3-4	1-4	1-4	1-4

Table 3. – Morphometric measurements (all in mm) of female specimens of species in the *Mantidactylus asper* group. Abbreviations as given in *Materials and methods* and in the caption to tab. 1. The measurements of *M. asper* are given separately for populations from north-eastern (NE, Tsaratanana, Marojejy) and central eastern (CE) Madagascar. *n* is the number of measured specimens. Measurements are given as mean ± standard deviation (range in parentheses). Relative hindlimb length (RHL) is coded as follows: when adpressed along body, the tibiotarsal articulation reaches (1) the nostril, (2) the snout tip, (3) beyond the snout tip or (4) widely beyond the snout tip.

Species	*M. asper* (CE)	*M. asper* (NE)	*M. spinifer*	*M. ambohitra*	*M. luteus*	*M. plicifer*
n	11	2	14	12	4	9
SVL	29.1 ± 0.8 (28.2-30.5)	33.2 ± 0.1 (33.1-33.3)	35.4 ± 1.5 (32.1-38.3)	35.2 ± 0.8 (32.4-38.5)	44.1 ± 2.6 (40.8-47.0)	46.9 ± 1.9 (44.6-49.8)
HW	9.2 ± 0.4 (8.6-10.0)	11.1 ± 0.7 (10.6-11.6)	11.5 ± 0.6 (10.7-12.3)	11.9 ± 0.9 (10.0-13.2)	16.0 ± 1.2 (15.1-17.8)	16.8 ± 0.7 (15.9-18.0)
HL	10.9 ± 0.4 (10.2-11.5)	12.0 ± 0.6 (11.6-12.4)	13.3 ± 0.5 (12.3-14.0)	13.3 ± 0.9 (11.9-14.7)	18.2 ± 1.2 (17.3-19.9)	18.6 ± 1.0 (17.4-19.8)
TD	2.1 ± 0.2 (1.8-2.4)	2.9 ± 0.2 (2.7-3.0)	2.5 ± 0.2 (2.2-2.8)	2.6 ± 0.2 (2.3-3.0)	3.1 ± 0.3 (2.8-3.4)	2.6 ± 0.2 (2.4-3.1)
ED	3.5 ± 0.2 (3.2-3.8)	3.8 ± 0.2 (3.6-3.9)	4.1 ± 0.2 (3.7-4.3)	4.1 ± 0.3 (3.6-4.5)	5.4 ± 0.4 (5.0-6.0)	5.6 ± 0.4 (4.8-6.1)
END	3.0 ± 0.2 (2.8-3.2)	3.3 ± 0.1 (3.2-3.3)	3.5 ± 0.2 (3.3-4.1)	3.3 ± 0.2 (2.8-3.6)	4.8 ± 0.2 (4.6-5.0)	4.8 ± 0.3 (4.4-5.3)
NSD	1.9 ± 0.2 (1.5-2.3)	2.0 ± 0.5 (1.6-2.3)	2.5 ± 0.2 (2.1-2.7)	2.1 ± 0.2 (1.6-2.4)	2.8 ± 0.1 (2.7-3.0)	3.1 ± 0.3 (2.7-3.7)
NND	2.3 ± 0.3 (1.8-2.8)	3.0 ± 0.0 (3.0-3.0)	2.5 ± 0.2 (2.2-3.0)	2.8 ± 0.2 (2.5-3.2)	3.7 ± 0.2 (3.5-3.9)	4.5 ± 0.2 (4.2-5.0)
FORL	19.5 ± 1.0 (17.5-20.8)	23.1 ± 0.6 (22.6-23.5)	24.1 ± 0.9 (22.2-25.3)	24.9 ± 1.4 (22.8-26.9)	27.9 ± 3. (25.1-31.8)	29.7 ± 1.2 (28.1-31.7)
HAL	9.0 ± 0.5 (8.1-9.6)	10.8 ± 0.4 (10.5-11.0)	10.9 ± 0.5 (10.1-11.7)	11.5 ± 0.8 (10.2-12.6)	13.1 ± 1.1 (12.2-14.6)	14.0 ± 0.6 (12.8-14.6)
HIL	55.6 ± 1.8 (51.6-57.8)	64.7 ± 0.6 (64.2-65.1)	66.0 ± 2.8 (60.3-69.9)	71.9 ± 3.1 (67.3-75.7)	87.6 ± 4.9 (80.4-90.9)	90.6 ± 3.9 (85.1-96.2)
FOTL	24.2 ± 1.0 (22.4-25.4)	28.1 ± 0.1 (28.0-28.2)	28.4 ± 1.0 (26.8-30.4)	31.1 ± 1.5 (28.6-33.2)	39.1 ± 2.1 (36.1-40.9)	39.8 ± 1.7 (37.5-42.7)
FOL	15.8 ± 0.8 (14.0-17.2)	19.5 ± 0.2 (19.3-19.6)	18.7 ± 0.7 (17.5-20.0)	21.1 ± 0.8 (20.0-22.4)	25.4 ± 1.8 (22.9-27.2)	25.7 ± 1.1 (23.7-27.6)
IMTL	1.1 ± 0.2 (0.8-1.4)	1.2 ± 0.2 (0-1.3)	1.4 ± 0.2 (1.2- ?)	1.3 ± 0.2 (0.9- 5)	7 ± 0.2 (1.5- 9)	1.8 ± 0.3 (1.4-2.2)
IMTW	0.7 ± 0.2 (0.5-1.0)	0.8 ± 0.2 (0.6-0.9)	0.9 ± 0.1 (0.7- 1)	0.7 ± 0.1 (0.5-1.0)	0.9 ± 0.1 (0.7- 0)	1.0 ± 0. (0.9-1.2)
TL1	3.0 ± 0.3 (2.5-3.5)	3.9 ± 0.3 (3.7-4.1)	3.7 ± 0.3 (3.2-4.4)	4.0 ± 0.3 (3.5-4.4)	5.0 ± 0.6 (4.1-5.6)	5.1 ± 0.4 (4.6-5.6)
RHL	1-4	3-4	1-4	3-4	3-4	2-4

with some reservations in *M. spinifer* (MNHN 1972.551-554). It contains specimens larger than typical *M. asper*, with more distinctly expressed spines and tubercles (two tarsal spines clearly recognizable) and a more distinct ventral contrast of white and dark coloration. These character states remind those of *M. spinifer* (see below). However, the specimens are still smaller than typical representatives of the species, and the ventral pattern contrast is less expressed. We here tentatively follow their assignation to *M. spinifer* as suggested by Blommers-Schlösser & Blanc (1991), but it should be kept in mind that they are intermediate between *M. spinifer* and *M. asper* in size and expression of ventral pattern contrast. The species is therefore known from (1) the Chaînes Anosyennes and (2) Ivohibe.

Natural history and advertisement call. – Unknown.

Mantidactylus ambohitra n. sp.

(fig. 3c-f)

Holotype. – ZSM 1084.2001 (originally ZFMK 57418), adult male, Montagne d'Ambre, collected by Frank Glaw, Nirhy Rabibisoa and Olivier Ramilison on 14-17 March 1994.

Paratypes. – MNHN 1893.244-245 (two females) from Montagne d'Ambre, MNHN 1893.246 (female), 1893.248 (male), 1893.249-250 (two females), 1893.252 (female), 1893.253 (juvenile), 1991.3148 (previously 1893.246A; female), all from Mararaomby (Montagne d'Ambre), sent to the Paris museum by Alluaud and Belly in 1893, MNHN 1972.573 (female) from Montagne d'Ambre, MNHN 1975.314 (female), 1975.322 (female), 1975.325 (female), 1975.329 (female), 1975.330-331 (two males) from Les Roussettes (Montagne d'Ambre), all without precise collecting data, MTKD 37424 (male) from Montagne d'Ambre, ZFMK 57419 (female) from Montagne d'Ambre, with same collecting data as holotype, ZFMK

62204-62205 (two subadults), collected by J. Steinbrecher on 26 November 1995 at Montagne d'Ambre.

Diagnosis. A member of the genus *Mantidactylus* based on the presence of femoral glands and absence of nuptial pads in males. Assigned to the *Mantidactylus asper* group in the subgenus *Gephyromantis* based on: (1) blackish paired subgular vocal sacs in males; (2) inner and outer outer dorsolateral ridges, (3) (small) heel spines; and (4) general similarity with other species of the group. The species is in several characters intermediate between *M. asper* and *M. spinifer* on the one hand, and *M. luteus, M. plicifer* and *M. sculpturatus* on the other hand. It is distinguished from *M. asper* and *M. spinifer* by its largely uniformly colored ventral side, a lower amount of dermal spines, less extended webbing and less prominent dorsolateral ridges. It is distinguished from *M. luteus, M. plicifer* and *M. sculpturatus* by smaller body size (male SVL 34-37 mm vs. 36-48 mm), less prominent inner dorsolateral ridges, small size of heel spines and supraocular spines, presence of an outer metarsal tubercle and occasional occurrence of interocular tubercles.

Etymology. Derived from *Ambohitra*, the Malagasy name for the Amber Mountain (Montagne d'Ambre), the type locality of the species. The name is used as invariable noun in apposition to the generic name.

Description of the holotype. – Adult male, SVL 35.8 mm (fig. 3c-d). For measurements, see tab. 1. Body slender; head slightly longer than wide, distinctly wider than body, snout rounded in dorsal and lateral views, nostrils directed laterally, slightly protuberant, much nearer to tip of snout than to eye; canthus rostralis distinct, concave; loreal region concave; tympanum distinct, elliptical (slightly higher than wide), 67 % of eye diameter; supratympanic fold very distinct, straight; tongue ovoid, distinctly bifid posteriorly, vomerine teeth distinct, in two rounded aggregations, positioned posterolateral to choanae, choanae rounded. Arms slender, subarticular tubercles single, one outer, central, and inner metacarpal tubercles present, fingers without webbing, relative length of fingers 1 < 2 < 4 < 3, second finger distinctly shorter than fourth, finger disks distinctly enlarged, nuptial pads absent. Hindlimbs slender, tibiotarsal articulation reaching widely beyond snout tip when hindlimb is adpressed along body, lateral metatarsalia separated by webbing, inner metatarsal tubercle distinct, outer metatarsal tubercle small but recognizable, webbing formula between toes 1(1), 2i(2), 2e(0.75), 3i(2), 3e(1), 4i(2), 4e(1.75), 5(0.25), relative toe length 1 < 2 < 3 < 5 < 4, third toe clearly shorter than fifth toe. Skin on the upper surface smooth, dorsolateral folds present but weakly expressed and not very prominent, inner dorsolateral folds present, starting ca. 2.5 mm behind the eyes and fading on the anterior back, outer dorsolateral folds running from ca. 4 mm posterior to the supratympanic fold to the inguinal region. Two distinct, longitudinal interocular tubercles, of same color as surrounding skin; supraocular tubercles present, supraocular spines and heel spine present but small. Ventral skin smooth on throat, slightly granular on posterior belly. Femoral glands very poorly delimited and very indistinct from both external and internal views, a patch of indistinct granules visible from internal view.

Dorsal coloration in preservative dark brown with a weakly defined vertebral region of lighter beige brown color. Posterior fifth of the dorsum and dorsal surface of the hindlegs light brown. One distinct and four indistinct dark brown crossbands on femur, one indistinct and three distinct bands on tibia, and five indistinct bands on tarsus and foot. Dorsal color of

forelimbs irregularly dark and light brown. On the flanks, the dark dorsal color fading gradually into the light ventral color. Head sides dark brown except an ill-defined light band running from the anterior eye corner to the upper lip. Ventrally cream-white with some weak symmetrical brown markings in the chest region. Throat cream-white, the inflatable lateral parts of the vocal sac black. In life, color was similar to that in preservative, the iris being light brown in its upper part, reddish brown laterally, and greyish brown in its lower part.

Variation. — The available specimens are largely in mediocre state of preservation, especially the MNHN specimens that were collected more than 100 years ago. Nevertheless, a relatively large variability of morphology (dorsal dermal structures) and coloration could be assessed. ZFMK 57419 (fig. 3e) has a strongly contrasted dorsal pattern of dark dorsolateral stripes on a light brown back. A further specimen (fig. 3f, not collected) had a light reddish brown head surface with a triangular posterior end, a pattern also known in *Mantidactylus luteus* (GLAW & VENCES, 1994: color plate 93) and other representatives of the genus. Another specimen (not collected) had a broad and sharply delimited median light stripe on the dorsum. The inner and outer dorsolateral ridges are always present but usually weakly expressed and often discontinuous. The inner dorsolateral ridges generally begin 2-3 mm behind the eyes. In some specimens, one or two pairs of indistinct ridge-like interocular tubercles are seen, but usually they are absent. Heel spine and supraocular spines are small, and often reduced to tubercles; tarsal spines are absent. Males have rather indistinct femoral glands. Humeral protuberances are not visible in the available material. Webbing in most specimens is rather developed, reaching almost the fifth toe disk, although it is less extended in other specimens (formula 0.75-0). The outer metatarsal tubercle is always visible though generally small. The three available juvenile paratypes already show some of the characteristics of *M. ambohitra* (e.g., not very prominent dorsolateral ridges, presence of ridge-like interocular tubercles).

Significant intersexual differences (Mann-Whitney *U* tests) were detected in relative length of fore- ($P < 0.05$) and hindlimbs ($P < 0.005$) and in relative length ($P < 0.05$) and height ($P < 0.005$) of the inner metatarsal tubercle, but not in relative tympanum diameter or SVL. Limbs are longer in females than in males, which is a rather uncommon state in Malagasy frogs; the inner metatarsal tubercle is longer and higher in males. Male/female size ratio is 102 %.

Further material. — MNHN 1893.243 (Montagne d'Ambre) is a large male specimen which reminds *Mantidactylus pliciferus* by size (SVL 44.8 mm) and by its large, distinct femoral glands. The probably subadult female MNHN 1975.324 (Les Roussettes) reminds *M. luteus* rather than *M. ambohitra*. As both specimens are in poor states of preservation, it is not possible to make a definitive statement on their identity. It is possible, however, that more than one representative of the *M. asper* group occurs at Montagne d'Ambre.

Three further specimens agree morphologically with *M. ambohitra* but are not included in the type series due to dubious or lacking information on their collecting locality. The male MNHN 1975.326 is labeled as originating from "Ifaty", but we consider it as very improbable that this refers to Ifaty in extremely arid south-western Madagascar (close to Toliara). The female MNHN 1975.332 has no locality information. Both these specimens bear numbers subsequent to small series originating from the Montagne d'Ambre region. The female MNHN 1973.896 was collected, according to the MNHN catalogue, by C. P. Blanc on 16 July 1972 at Marojejy (300 m elevation); however, its "hard" state of fixation is similar to that of

specimens from Montagne d'Ambre (e.g. MNHN 1975.332) rather than to the more flexible, obviously formalin-fixed *M. luteus* specimens from Marojejy, collected also by C. P. Blanc in July 1972 (MNHN 1973 897-902).

Distribution. – The species is so far reliably known only from (1) its type locality, Montagne d'Ambre in far northern Madagascar.

Natural history. – We observed specimens during the day on the forest floor. J. Köhler (pers. comm.) observed calling males in November in the evening (20-22 h and later) during light rain, calling from bushes at the forest edge, ca. 60-150 cm above the ground. Inflated vocal sacs were paired subgular (fig. 3f).

Advertisement call. – Unknown.

Mantidactylus luteus Methuen & Hewitt, 1913

(fig. 5a-b)

Mantidactylus luteus Methuen & Hewitt, 1913. – *Name-bearing type*: holotype, by original designation, TM 10077, adult male collected by Herschell-Chauvin. – *Type locality*: Folohy. – *Other types*: paratypes, TM 10095-10101, two adult males, two adult females and three juveniles, and TM 10094 (exchanged with another collection according to TM catalogue).

Identity. – The type series, as examined by us in 1998, agrees morphologically with the populations attributed to *M. luteus* and inhabiting the low-elevation areas of the Malagasy east coast. This form is morphologically recognizable by: (1) rather small size, (2) distinct but rather small femoral glands in males; and (3) generally uniformly whitish venter without distinct dark chest markings. The holotype has a SVL of 41.3 mm, FGL of 6.4-6.8 mm and FGW of 1.6-1.9 mm (W. Haacke, pers. comm. in 2001), thus within the range of other male specimens herein assigned to the species (tab. 2). We will, in the following, provide a detailed morphological description of *M. luteus*, and only mention differences from this pattern in the subsequent sections on *M. plicifer* and *M. sculpturatus*.

Material examined. – MNHN 1975.323 (Kianjavato), MNHN 1972.1435 (Ambana-Soavala, Chaînes Anosyennes), MNHN 1972.1418 (Camp V, Chaînes Anosyennes), MNHN 1973.897-902, 907, 908, 910 (Marojejy, alt. 300 m), MNHN 1973.906 (Marojejy, alt. 1300 m), MNHN 1973.909 (Marojejy, alt. 600 m), TM 10077, 10095-10101 (holotype and paratypes, Folohy), ZFMK 47222, 47290-47291, 52711, 52713-52714 (Nosy Boraha); ZFMK 52715, 66674 (Nosy Mangabe).

Morphology. – The description provided here refers to male specimens from Marojejy (MNHN 1973.897, 1973.899-902, 1973.906-908), Nosy Mangabe (ZFMK 66674) and Nosy Boraha (ZFMK 52714) which form a morphologically homogeneous group. Morphology and attribution of other specimens is discussed in the section on distribution. Inner and outer dorsolateral ridges present and usually continuous, the inner ridge being more prominent than the outer ridge. Inner dorsolateral ridges generally beginning above the eye and running onto the central dorsum, ending in various modes, either fading or curving medially or laterally, sometimes continued as indistinct undulating structures towards the inguinal region. Outer dorsolateral ridges generally beginning in the shoulder region where the inner ridges end (fig. 1). No connecting dorsal ridge, no interocular tubercles. Supraocular tubercles and a



Fig. 5. – Photographs of *Mantidactylus luteus*, male from Nosy Boraha, in dorsolateral and ventral views (a-b), *M. plicifer* male from Ranomafana (ZFMK 62305) in dorsolateral and ventral views (c-d), and *M. sculpturatus*, male from Andasibe (ZFMK 53688) in dorsolateral and ventral views (e-f).

few small supraocular spines present. Usually one distinct supraocular spine coinciding with the origin of the inner dorsolateral ridge. A distinct heel spine, no tarsal spines. Males with small but distinct femoral glands (see tab. 2), in MNHN 1973.899 (Marojejy), the gland on one femur, in internal view, composed of 16 granules of 0.4-0.9 mm diameter each, in ZFMK 66674 (Nosy Mangabe), of 29 granules of 0.4-0.6 mm. Vocal sac paired subgular. A strongly expressed humeral protuberance in males, lacking in females. Webbing in most specimens reaching the disc of the fifth toe, resulting in webbing formulas of 5(0) or 5(0.25). One inner and two rather weakly expressed, similarly-sized outer metacarpal tubercles, the latter two in contact with each other. A distinct inner but no outer metatarsal tubercle.

Significant intersexual differences in the whole sample attributed to *M. luteus* were found in SVL and in relative length (Mann-Whitney *U* test, $P < 0.05$) and height ($P < 0.005$) of the inner metatarsal tubercle (longer and higher in males), but not in relative tympanum diameter or relative length of limbs. Male/female size ratio is 89 %.

Coloration. Dorsally generally uniformly greyish brown, sometimes with some shades and indistinct markings of lighter or darker brown. Usually with at least a partial black bordering of the inner dorsolateral ridges towards the flanks. Two further black spots often present at the origin of the outer dorsolateral ridges. Indistinct but often well-delimited crossbands on the hindlimbs (5-7 on femur, 3-7 on tibia, 4-10 on tarsus and foot). Ventral color uniformly cream, including the limbs. Only some specimens with faint brownish markings on chest and (in males) on throat. Lateral, inflatable parts of the (paired subgular) vocal sacs black.

Distribution. Beside male specimens from Marojejy, Nosy Mangabe and Nosy Boraha, we also attribute several vouchers to *M. luteus*. Two males from the Chaînes Anosyennes (MNHN 1972.1418 and 1972.1435), which were collected syntopically with *M. plicifer* (see below), differ from that species by their completely uniform chest, smaller size and smaller femoral glands (consisting of 24 granules of 0.4-0.6 mm diameter in MNHN 1972.1435). The male MNHN 1975.323 (Kianjavato) also agrees in having distinct femoral glands with 21 large granules. The females ZFMK 52711 (Nosy Boraha) and ZFMK 52715 (Nosy Mangabe) are rather large (SVL 45.0 and 47.0 mm, respectively), and would therefore agree better with *M. plicifer* by size. However, the almost uniform whitish venter of ZFMK 52711 and the very faint chest mottling of ZFMK 52715 agree with the state in *M. luteus*. As so far no records of *M. plicifer* exist for central-eastern or north-eastern Madagascar, we assign these female specimens to *M. luteus*. We attribute also the juveniles MNHN 1972.909 and 910 (Marojejy) to this species, as neither *M. plicifer* nor *M. sculpturatus* are known from this region. A further locality is Foulpointe which is based on a single voucher (ZMA 6725) which agrees with *M. luteus* in body size and femoral gland proportions according to a personal communication of F. Andreone. Summarizing, specimens attributable to *M. luteus* are from: (1) Marojejy; (2) Nosy Mangabe; (3) Nosy Boraha; (4) Foulpointe; (5) Folohy (type locality); (6) Kianjavato; and (7) the Chaînes Anosyennes (including Ambana-Soavala and Camp V). All these localities are at low elevations along the Malagasy east coast; only one specimen (MNHN 1973.906) is catalogued as originating from 1300 m on the Marojejy massif, while the other specimens from this locality were collected at 300-600 m elevation.

BLOMMERS-SCHLÖSSER & BLANC (1991) additionally recorded the species from a number of further localities, namely Les Roussettes (Montagne d'Ambre), Ambalamarovandana, Marovitsika and Antsalova. The available Montagne d'Ambre specimens are here all referred to the new species *M. ambohitra*, although at least two of these are actually morphologically similar to *M. luteus*, and the possible occurrence of this or a similar species at Montagne d'Ambre warrants further research (see section on *M. ambohitra*). The available material from Ambalamarovandana may be attributable to *M. sculpturatus* or *M. luteus* (see below). The locality Marovitsika forest (Pic Ivohibe) is based on juvenile specimens only. The locality Antsalova (Antsingy) is corroborated by one MNHN voucher from this site catalogued as *M. luteus*. This specimen (MNHN 1975.327), however, has no dorsolateral ridges and clearly agrees in general morphology with *Mantidactylus corvus* and *M. pseudoasper* (subgenus *Phylacomantis*), two morphologically similar species of which one (*M. corvus*) has been

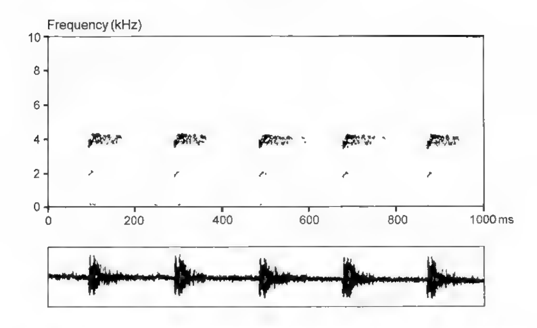


Fig. 6. – Sonagram and oscillogram of part of a call (five notes of a note series) of *Mantidactylus luteus* from Marojejy.

described from western Madagascar (Isalo). Occurrence of *M.* cf. *pseudoasper* in the Antsingy forest is also corroborated by MSNG 49087 which was the origin of the tissue samples used for DNA analyses herein.

Natural history. – Calling activity was mainly nocturnal but sometimes started before dusk. In such cases, the calls were emitted from the ground. Calling activity increased with progress of dusk, and at night specimens generally called from leaves 1-2 m above the ground. We never observed calling specimens gathering at or close to water bodies.

Advertisement call. – Calls were series of short, relatively melodious notes (fig. 6). Each note did correspond to one expiration. Between notes, the vocal sac did not remain distinctly inflated, although a slight inflation was noted when a call series was about to start. Calls from Marojejy (Camp 1) were recorded on 27 March 1994, 17:30 h, at 22°C air temperature. They contained up to 21 notes. Note duration was 22-24 ms (23 ± 1 ms, $n = 5$), duration of intervals between notes was 170-180 ms (173 ± 5 ms, $n = 4$). Note repetition rate was 5.0-5.5 ms. Calls from Nosy Boraha as described by Glaw & Vences (1992) were similar and are here re-described. They were recorded on 8 March 1991 at ca. 22°C air temperature. Note duration was 44-59 ms (51 ± 5 ms, $n = 8$), interval duration 127-236 s (156 ± 40 ms, $n = 7$), and note repetition rate 4.3-5.0 per second.

On 28 March 1994, distress calls were emitted by a specimen from Marojejy when handled. Two calls had a duration of 1600 ms and 1663 ms. Frequency was 1650-10000 Hz.

respectively 0-10000 Hz, and showed the frequency band pattern typical for anuran distress calls.

Mantidactylus plicifer (Boulenger, 1882)

(fig. 5c-d)

Rana plicifera Boulenger, 1882. *Name-bearing type*. lectotype, by present designation, BMNH 1882.3.16.58, adult male collected by W. D. Cowan. *Type locality*. 'East Betsileo" according to the original description. *Paralectotypes*. BMNH 1882.3.16.57, female and 1882.3.16.56 and 59, two subadult specimens, with same collecting data as lectotype.

Comment. The current re-definition of the species *M. plicifer* is based on characters (size and structure of femoral glands) recognizable in males only. As only one of the original syntypes of *Rana plicifera* is a male, its present designation as lectotype is necessary to reach taxonomic stability in a group of extremely similar species (*M. luteus*, *M. plicifer*, *M. sculpturatus*).

Identity. – Our field observations demonstrated syntopic occurrence of a smaller and a larger *M. luteus*-like species at Ranomafana, males of the larger species reaching 44.2-44.4 mm SVL. Also in the MNHN sample from the Chaînes Anosyennes, a larger and a smaller form could be distinguished, males of the larger form ranging from 43.6 to 48.3 mm SVL. One distinctive character of the large form at both sites were its consistently large and distinct femoral glands. Based on this character, we consider the large specimens as *Mantidactylus plicifer*, fig. 7 shows that they agree with the lectotype of *Rana plicifera* in relative femoral gland size, although the type is distinctly smaller (38.8 mm SVL, see tab. 1-2). The difference both in SVL and in relative length and width of femoral glands (ratio FGL/SVL and FGW/SVL) was highly significant between *M. plicifer* and *M. luteus* ($P < 0.005$).

Material examined. BMNH 1882.3.16.56-59 (East Betsileo, lectotype and paralectotypes), MNHN 1972.1404 (Ambana-Soavala, Chaînes Anosyennes), MNHN 1972.1405, 1972.1407-1408, 1972.1410, 1972.1412-1414, 1972.1419-1422, 1972.1424-1425, 1972.1427, 1972.1429, 1972.1431 (Camp V, Chaînes Anosyennes), MNHN 1972.1436-1437 (Camp IV, Chaînes Anosyennes), ZFMK 62305-62306 (Ranomafana).

Morphology and diagnosis. Beside the larger size of most specimens as compared to *M. luteus*, the most important morphological character to identify *M. plicifer* is the large size of its femoral glands (see *Identity* section). In internal view, a gland of the lectotype contained about 45 granules. In one specimen from Ranomafana (ZFMK 62306), a gland was composed of 47 granules of 0.5-0.7 mm in diameter. In one specimen from the Chaînes Anosyennes, a gland was composed of 55 granules of 0.4-0.8 mm in diameter.

Beside this character, the morphology of *M. plicifer* is extremely similar to *M. luteus*. The differences mentioned by BLOMMERS-SCHLÖSSER & BLANC (1991) in their key to *Mantidactylus*, namely webbing (less developed in *M. plicifer*) and heel spine (only a tubercle present in *M. plicifer*) are not suited to distinguish both species. The webbing is variable in *M. plicifer*. For instance, it reaches the disk of the fifth toe in ZFMK 62306, but only inbetween the disk and the external subarticular tubercle in ZFMK 62305, resulting in webbing formulas for the fifth toe of 5(0) vs. 5(0.5). And the presence of a heel spine appears to be highly dependent on

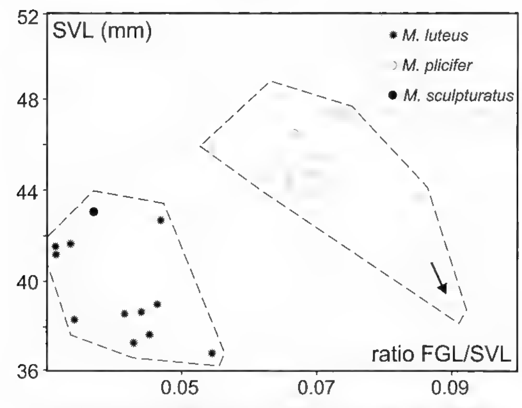


Fig. 7. – Scatterplot of snout-vent length (SVL) and relative femoral gland length (ratio FGL/SVL) in *Mantidactylus luteus*, *M. plicifer* and *M. sculpturatus*. Note the clear distinction of *Mantidactylus plicifer* from the other two species by its larger femoral gland size. Most *M. plicifer* can also be distinguished by their larger SVL, the lectotype of *M. plicifer* (marked by an arrow), which in contrast is small-sized, shares with the other specimens its large femoral glands.

the state of fixation and preservation of the specimens. So, a heel spine is clearly visible in the formalin-fixed *M. plicifer* from Chaines Anosyennes, but this structure is only rudimentary and faintly recognizable in the ethanol-fixed specimens from Ranomafana. The outer metatarsal tubercle, absent in *M. luteus*, is sometimes visible as small rudiment in formalin-fixed *M. plicifer*. The pair of outer metacarpal tubercles are often indistinct in *M. plicifer* as in *M. luteus*, but when recognizable, the outermost tubercle is distinctly smaller and more elongate.

Color and pattern variation is as follows. Many specimens with a tendency of a lighter lateral coloration and a darker dorsal coloration, more or less sharply separated by the dorsolateral ridges, this contrasted pattern very distinct in a few specimens (e.g. MNHN 1972.1427) which have light brown to beige flanks and dark brown central dorsum and head surfaces, both colors sharply separated by the dorsolateral ridges. In this specimen, head also laterally beige, with a broad vertical band running from the eye to the upper lip. In some specimens, head laterally with a broad light beige band along the upper lip, bordered sharply

by a dark brown band along the canthus rostralis. Venter cream whitish, with a few brownish markings usually present in the chest region. Throat largely covered by faint brown pigment in many males (except a longitudinal light median band). Vocal sacs blackish.

Intersexual differences in SVL and relative tympanum size are close to significance (Mann-Whitney *U* test; $P < 0.07$), males being smaller and having relatively larger relative tympanum sizes than females. Highly significant differences were found in relative length and height of the inner metatarsal tubercle ($P < 0.001$; longer and higher in males), while relative limb length did not differ significantly between sexes. Mean male/female size ratio is 96 %.

Distribution. – Beside the unprecise type locality East Betsileo, the species is reliably known from (1) Ranomafana and (2) the Chaînes Anosyennes. BLOMMERS-SCHLÖSSER & BLANC (1991) listed six additional localities for the species: Tsaratanana, Marojejy, Ambohitantely, Mandraka, Ambalamarovandana, Marovitsika. We could not locate any voucher for the Ambohitantely locality in the MNHN or ZMA collections. The specimens from Tsaratanana, Marojejy and Mandraka, determined as *M. plicifer* by R. Blommers-Schlösser according to the MNHN catalogue, are here all referred to *M. asper* (see also GLAW & VENCES, 1994, for the Tsaratanana vouchers). The specimens from Marovitsika are juveniles that cannot be reliably determined, while those from Ambalamarovandana are here assigned to *M. sculpturatus* in a preliminary way (see below).

Natural history. – Calls were heard during dusk from the vegetation in rainforest. Calling males were sitting ca. 50 cm above the ground. No water bodies were observed in the surroundings.

Advertisement call. – Recordings were done on 2 March 1996, 18.15 h, at 23°C air temperature in the Ranomafana National Park. Single notes as well as short series of up to five notes (fig. 8) were emitted. Note duration was 121-148 ms (134 ± 10 ms, $n = 5$), duration of intervals between notes was 492-559 ms (535 ± 31 ms, $n = 4$). Since intensity faded continuously at the end of each note, measuring of note duration was difficult, and it would also be possible to consider note durations as longer (and, correspondingly, interval durations as shorter). Frequency was 1200-4000 Hz, dominant frequency 2700-3300 Hz.

Mantidactylus sculpturatus Ahl, 1929

(fig. 5e-f)

Mantidactylus sculpturatus Ahl, 1929. – *Name-bearing type*: holotype, by monotypy, ZMB 30515. – *Type locality*: "Nordwest-Madagascar" according to original description (probably erroneous). – *Other types*: none.

Identity. – At mid-altitude localities of eastern Madagascar, a species occurs which is extremely similar to *M. luteus* by morphology. It is, however, distinguished by its unharmonious (vs. melodious) advertisement calls, its indistinct femoral glands, and a relatively high genetic divergence (see below). We here revalidate the name *Mantidactylus sculpturatus* for this species based on the following rationale. (1) The type of *M. sculpturatus* is a female of 37.5 mm SVL; its morphology totally corresponds to species previously assigned to *M. luteus*,

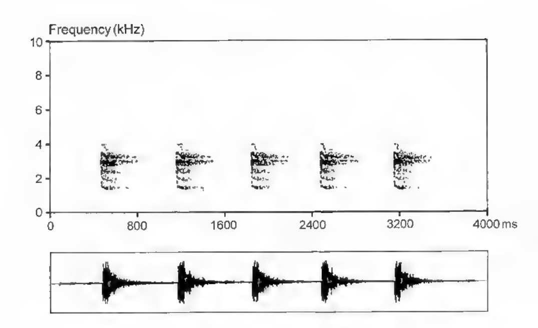


Fig. 8. – Sonagram and oscillogram of part of a call (five notes of a note series) of *Mantidactylus plicifer* from Ranomafana.

and its size agrees with the mid-altitude *luteus*-like species but not with the larger species *M. plicifer*. (2) AHL (1929) described *M. sculpturatus* from a specimen that was collected by J. M. Hildebrandt, and that was reported to originate from northwestern Madagascar. However, no species close to *M. luteus* is so far known from this region, except an undescribed species from the Manongarivo Reserve collected by C. J. Raxworthy (deposited in the London museum) and by D. Rakotomalala (pers. comm.). These Manongarivo specimens, however, have distinct interocular tubercles in males and females which are absent in the type of *M. sculpturatus*. As with other anuran species collected by J. M. Hildebrandt in this region, it is probable that some labeling errors occurred either by Hildebrandt itself or when the specimens were entered in the Berlin Museum after Hildebrandt's death in Madagascar in 1881 (VENCES & GLAW, submitted). (3) Beside localities in northwestern Madagascar, Hildebrandt collected at sites in central eastern Madagascar but apparently not at low altitudes along the east coast (BIENTJE, 1998). It is therefore probable that the *M. sculpturatus* type was collected at a mid-altitude eastern locality. We are aware that these arguments do not suffice to fully clarify the identity of *M. sculpturatus*, but its present re-definition appears as most parsimonious solution and avoids the description of the mid-altitude *luteus*-like form as a new species.

Note. – BLOMMERS-SCHLÖSSER & BLANC (1991) stated that the "type" of *M. sculpturatus* was lost. In the meantime, the holotype has been rediscovered in the Berlin museum.

Material examined. – ZFMK 53688-53689 (Andasibe), ZFMK 62304 (Ranomafana), ZMB 30515 (holotype).

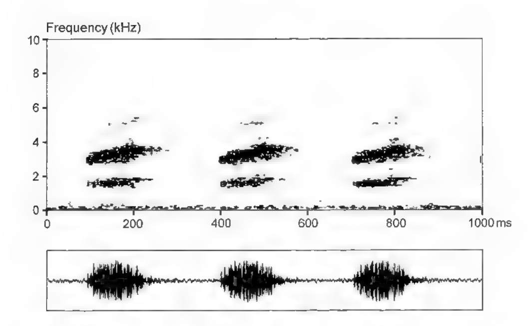


Fig. 9 Sonagram and oscillogram of a call (three notes of a note series) of *Mantidactylus sculpturatus* from Ranomafana

Morphology and diagnosis. – By size and general morphology, this species is similar to *M. luteus*. Femoral glands are indistinct in most specimens, in ZFMK 62304 (Ranomafana), an adult male collected while calling and therefore in sexually mature and active state, no femoral glands at all were recognizable in external or internal view. The male ZFMK 53688 (Andasibe) had 26 scattered granules visible in internal view of a gland. These granules, however, were smaller than in *M. luteus* (0.3-0.4 mm in diameter).

In the available material, no recognizable outer metatarsal tubercle. Webbing reaching the disk of the fifth toe or slightly below, resulting in a webbing formula of 5(0)-5(0.25). A small heel spine, and two external metacarpal tubercles of approximately similar size. General coloration as in *M. luteus*, the specimen ZFMK 62304 from Ranomafana having a broad white streak along the upper lip bordered by a blackish streak running under the canthus rostralis. This specimen additionally with a curved white streak running transversally above the cloacal region. Venter uniformly light, with very faint brownish pigment on the chest in some specimens.

Distribution. – The species is reliably known from: (1) Andasibe, (2) Ankeniheny (no voucher specimens collected); and (3) Ranomafana.

Natural history. – Calling males were observed at night, not concentrated around water bodies, 1-2 m high in the vegetation, in rainforest.

Advertisement call. – Calls from Ankeniheny were recorded on 18 December 1994, 21.45 h, at ca 22°C air temperature. They consisted of up to 22 unharmonious notes, but at the beginning

of calling activity single-note calls were common Following several of these, note-series were successively composed of an increasing number of notes. After such a call series, calling activity was often interrupted for some minutes; one call series from Andasibe lasted 20 s and showed the following pattern: 1-1-2-3-15 (numbers referring to notes per call). However, multi-note calls were emitted spontaneously as well. Note duration at Ankeniheny was 154-180 ms (168 ± 13 ms, $n = 5$), duration of intervals between notes was 126-163 ms (143 ± 18 ms, $n = 4$). Note repetition rate was 3.0-3.3 per second Calls from Andasibe (recorded on 12 January 1992 at 22°C air temperature) were similar, with a note duration of 90-120 ms, an interval duration of 250-260 ms, and a note repetition rate of 2.8/s (Glaw & Vences, 1994)

Calls from Ranomafana (fig. 9) were similar, too. Two analysed calls consisted of 15-17 notes and had a duration of 4463-5127 ms. Note repetition rate was 3.3-3.4/s. Note duration was 150-196 ms (173 ± 13 ms, $n = 10$), inter-note interval duration was 122-158 ms (139 ± 12 ms, $n = 10$). Frequency bands were recognizable between 1500 and 2000 Hz, 2800 and 4000 Hz, and 4800 and 5200 Hz. Dominant frequency was between 3200 and 3400 Hz

Further specimens of uncertain attribution

While the specimens listed in the respective sections above could be attributed to the recognized species with a certain reliability and were used to delimit distribution patterns (fig. 10), the following juvenile specimens (and thus the localities Vondrozo, Ivohibe, Sanga Sanga forest and Tolongoina) could be assigned to the complex of the three species *M luteus*, *M plicifer* or *M. sculpturatus*, but a specific determination was not possible. MNHN 1930.414 and MNHN 1991 3149-3150 (previously 1930 414A-B) (Vondrozo); MNHN 1972 556 (Ivohibe, Marovitsika forest), MNHN 1972.1434 (Ambana-Soavala); MNHN 1972 1406, 1972 1409, 1972.1411, 1972.1415-1417, 1972 1423, 1972 1426, 1972 1428, 1972 1430, 1972.1432-1433 (Camp V, Chaînes Anosyennes); MNHN 1972 1469 (Ambana-Camp IV, Chaînes Anosyennes); MNHN 1975.328 (Sanga Sanga forest), ZFMK 47252-47253 (Tolongoina) The same applies to an adult female (MNHN 1930 413) from Fort Carnot, (SVL 42 1 mm) which is in poor state of preservation and with largely faded pattern

A series from Ambalamarovandana (Andringitra, at 1530 m elevation, MNHN 1972 595-599) consists of two juveniles, one subadult, and two adult females with immature oocytes. By the size of the females (SVL 40 8 mm, MNHN 1972 595; 40 6 mm, MNHN 1972 596) and complete lack of dark pattern on throat and chest, they can be assigned to either *M. luteus* or *M. sculpturatus* rather than to *M plicifer*.

Three examined specimens probably belong to the *Mantidactylus asper* group but can not be determined further at present. (1) MNHN 1975.315 (Ambatofitoharanana) is a rather large female (SVL 42 9 mm) reminding *Mantidactylus asper* and *M ambohitra* It has very weakly expressed, straight dorsolateral ridges and apparently no markings on the venter The locality Ambatofitoharanana is located close to Fianarantsoa, at a rather high altitude of ca 1600 m. The specimen may represent a hitherto unknown species. (2) MNHN 1975 316 (Marojejy, no elevational information), an adult female (SVL 31 3 mm) with maturing oocytes recognizable by dissection, has two distinct pairs of ridge-like interocular tubercles, but only rudiments of dorsolateral ridges, instead, the dorsum is covered with irregular small

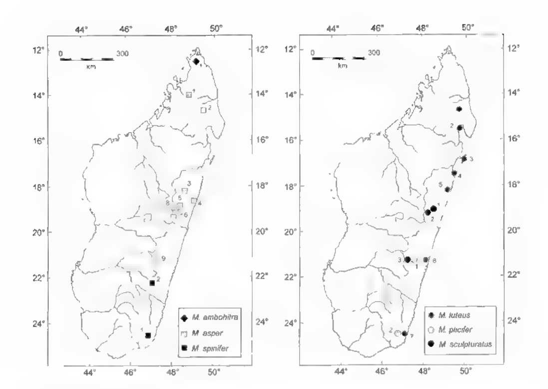


Fig. 10. Distribution maps of species in the *Mantidactylus asper* group. Locality numbers refer to those used in the text.

tubercles. The venter is uniformly light except two faint symmetrical brownish markings on the chest. This individual may represent a new species of *Mantidactylus* (*Gephyromantis*), but a description does not seem justified until further collections yield also male specimens. (3) MNHN 1895.257 is a juvenile specimen in poor state of preservation that reminds *M. asper*. It is remarkable because according to the MNHN catalogue it was collected on the west coast ("Côte Ouest"). However, we consider this locality information as dubious until the occurrence of the group at western localities is confirmed.

KEY TO SPECIES IN THE *MANTIDACTYLUS ASPER* GROUP

The following key allows identification of most specimens belonging to the *Mantidactylus asper* group. However, in some taxa (e.g., *M. luteus*, *M. plicifer*, *M. sculpturatus*), a reliable determination is only possible in adult males (after examination of femoral glands or advertisement calls). Considering the important variability of characters such as dorsolateral ridges within populations (e.g., of *M. asper* or *M. spinifer*), determinations based on single specimens should be always considered with caution.

1a. Moderately sized to large species (SVL 32-50 mm); ventrally uniformly cream-whitish, sometimes with brown mottling on chest and throat; tarsal spines and connecting dorsal ridge absent; interocular tubercles usually absent; outer metatarsal tubercle present or absent; webbing generally reaching closer to the disk of the fifth toe than to the first subarticular tubercle: webbing formula 5(0) to 5(0.5)........ 2

1b. Moderately sized species (SVL 27-38 mm); ventrally usually with distinct dark brown pattern (laterally delimiting a central bright white area on chest and sometimes belly; throat in males brown with a light median stripe); tarsal spines sometimes present; interocular tubercles generally present, outer metatarsal tubercle present; webbing generally closer to the first subarticular tubercle than to the disk of the fifth toe: webbing formula 5(0.5) to 5(0.75), rarely 5(0.25)............ 4

2a. Moderately sized species (SVL 32-39 mm); interocular tubercles sometimes present; supraocular spines small or in the form of tubercles only; dorsolateral ridges relatively irregular and indistinct; heel spine small and indistinct; outer metatarsal tubercle present, only known from far northern Madagascar (Montagne d'Ambre)................ *Mantidactylus ambohitra*

2b. Larger species (SVL 36-50 mm); interocular tubercles always absent; supraocular spines distinct, with one relatively large spine at the beginning of the inner dorsolateral ridge; inner dorsolateral ridge always distinct, heel spine distinct, outer metatarsal tubercle absent or rudimentary............ 3

3a. SVL 39-50 mm; femoral glands distinct, composed of 47-55 granules; calls composed of a slow series of unharmonious notes .... *Mantidactylus plicifer*

3b. SVL 36-47 mm, femoral glands small but distinct, composed of 16-29 granules; calls composed of a rapid series of melodious notes; known from eastern lowlands .... *Mantidactylus luteus*

3c. SVL 38-43 mm; femoral glands small and often indistinct or not recognizable, composed of 26 granules (if visible); calls composed of a rapid series of unharmonious notes; known from eastern mid-altitudes .... *Mantidactylus sculpturatus*

4a. Very granular dorsum with highly elevated and sharp ridges, connecting dorsal ridge often present; tarsal spines present and distinct; very distinct sharp dark brown-white contrast in the ventral pattern, extending onto the belly .... *Mantidactylus spinifer*

4b. Less granular dorsum; no connecting dorsal ridge; tarsal spines usually reduced to tubercles or absent, sharp brown-white contrast in the ventral pattern usually restricted to chest and/or throat .... *Mantidactylus asper*

Analysis of DNA sequences

A chi-square test did not contradict homogeneity of base frequencies across taxa (df = 51, $P > 0.9$). The PTP test resulted in a significant difference ($P = 0.01$) between the most parsimonious tree and trees generated from random permutations of the data matrix, demonstrating presence of significant phylogenetic signal. Of the total of 556 included characters, 358 were constant, 59 variable but parsimony-uninformative, and 139 variable and

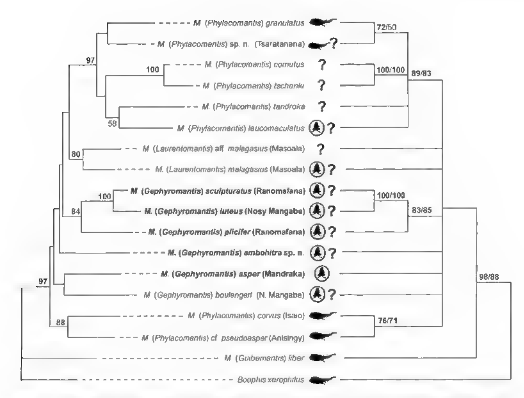


Fig. 11 Results of a Neighbor-joining (NJ, left) and a Maximum Parsimony (MP, right) analysis of 556 bp of a fragment of the mitochondrial 16S rRNA gene in 16 species of *Mantidactylus* belonging to the subgenera *Gephyromantis*, *Laurentomantis* and *Phylacomantis*. Species of the *M. asper* group are printed in bold. The MP cladogram is a strict consensus of eight equally most parsimonious trees (505 steps, consistency index 0.54, retention index 0.48). Numbers above branches are bootstrap values in percent of Neighbor joining (left) and Maximum Parsimony and Maximum Likelihood (right) analyses, respectively (2000, 2000 and 100 replicates). *Boophis xerophilus* was used as the outgroup. The symbols refer to presence of free-swimming or non feeding larvae (tadpole symbol) or direct development within the egg (egg symbol). Symbols with question marks refer to indirect evidence from calling behaviour, species which call around water bodies (brooks) may have tadpoles, while species calling independently from water probably have direct development.

parsimony-informative. MODELTEST proposed a Tamura-Nei substitution model (TrN + I + G) as best fitting the data, with a proportion of invariable sites of 0.4764, a gamma shape distribution parameter of 0.9064, and empirical base frequencies (A 0.3370, C 0.2328; G 0.1765, T 0.2536) and substitution rates (A-G: 5.3583, C-T 8.5036, all other rates: 1). The Maximum Parsimony analysis resulted in eight equally most parsimonious trees (505 steps, consistency index 0.54, retention index 0.48). A strict consensus of these is shown in fig. 11. Most splits in the topology were unresolved, resulting in several polytomies. The following clades were resolved: (1) a lineage containing the species of the *Mantidactylus granulatus* group in the subgenus *Phylacomantis* (sensu GLAW & VENCES, 1994), (2) within the *M.*

granulatus group, one clade containing *M. granulatus* and an undescribed species from Tsaratanana, and a second clade containing *M. cornutus* and *M. tschenki*, (3) a lineage containing the two species of the subgenus *Laurentomantis* included, (4) a clade containing *M. luteus*, *M. sculpturatus* and *M. plicifer*, (5) a clade containing *M. sculpturatus* and *M. luteus*; (6) a clade with the two species of the *Mantidactylus pseudoasper* group in the subgenus *Phylacomantis*, *M. pseudoasper* and *M. corvus*.

An identical topology was obtained by a second MP analysis after exclusion of all characters with gaps in one or more taxa. The NJ analysis with LogDet distances (fig. 11) and the ML analysis using the substitution model suggested by MODELTEST (not shown) supported the same clades. Both in the NJ and ML trees, the *M. pseudoasper* group was arranged basal to all other *Gephyromantis*, *Laurentomantis* and *Phylacomantis* species; sequentially, the species of *Gephyromantis* split off the phylogram, while the two *Laurentomantis* were placed as sister group of the *Mantidactylus granulatus* group.

Bootstrap analyses (Felsenstein, 1985) with 2000 replicates provided rather high support for most of the clades defined above (1-6); the sole exceptions were clade 2 which was not supported by values higher than 50 % in the NJ bootstrapping, and clade 3 which received low support (51 %) in the MP bootstrapping.

Pairwise sequence divergences among species of the subgenera *Gephyromantis*, *Phylacomantis* and *Laurentomantis* ranged from 3.8 to 16.4 %. Even the lowest values (3.8 % and 4.7 % between the species pairs *M. cornutus* – *M. tschenki* and *M. luteus* – *M. sculpturatus*) were distinctly higher than values so far identified between conspecific Malagasy frog populations (up to ca. 1.5 % in *M. granulatus*; M. Vences, unpublished).

Discussion

The distinctness of the three species *M. luteus*, *M. plicifer* and *M. sculpturatus* as re-defined here is well corroborated by their bioacoustic and genetic differentiation. Previous works (e.g., Blommers-Schlösser & Blanc, 1991) also recognized two of these species (*M. luteus* and *M. plicifer*), but their concept of *M. plicifer* was equivocal, and in large part based on specimens attributable to *M. asper*. We observed syntopic occurrence of two species (*M. plicifer* and *M. sculpturatus*) in the field at one site (Ranomafana), and preserved material provided evidence for syntopic occurrence of *M. plicifer* and *M. luteus* at the Chaînes Anosyennes. On the other hand, the morphological differences between these species are extremely faint, and at present no reliable characters are known which could diagnose their females or juveniles. This is in agreement with the situation in almost all groups of anurans in Madagascar; the emerging picture indicates that all forms which differ bioacoustically have a high genetic differentiation and must be regarded as valid species both under evolutionary and biological species concepts. Among *M. luteus*, *M. plicifer and M. sculpturatus*, the lowest genetic differences are found between *M. luteus* and *M. sculpturatus*, which were reliably grouped as sister taxa by the phylogenetic analysis. The apparent allopatric distribution of these species indicates an altitudinal segregation, *M. sculpturatus* inhabiting mid elevations and *M. luteus* low-elevations along the eastern coast. This example may indicate that sibling

species that segregate along elevational gradients in Madagascar are phylogenetically younger than those which occur in close sympatry (as *M. plicifer* – *M. luteus* or *M. plicifer* – *M. sculpturatus*).

The presence of a new species, *Mantidactylus ambohitra*, at Montagne d'Ambre in far northern Madagascar has already been suspected by GLAW & VENCES (1994), who figured a specimen from this locality as "*Mantidactylus* cf. *asper*". The isolated Montagne d'Ambre rainforest shares a rather large number of species with the eastern and north-eastern rainforests which, on the contrary, are not present in the north-western (Sambirano) region (RAXWORTHY & NUSSBAUM, 1994; RASELIMANANA et al., 2000), but the taxonomy of the Ambre populations has so far not been studied in detail. Our unpublished bioacoustic and genetic data indicate substantial differentiation of the Ambre populations of at least three other species shared with the east, namely *Heterixalus betsileo*, *Mantidactylus curtus* and *Mantidactylus liber*. At least some of these populations possibly merit a status as separate species, and may have originated by allopatric speciation in the isolated rainforest patch of the Ambre massif.

As the occurrence of *Mantidactylus luteus* in Antsalova was based on a misidentification of MNHN 1975.327 (actually belonging to *M. pseudoasper* or *M. corvus*), no reliable records of any species of the *M. asper* group and of the whole subgenus *Gephyromantis* exist at present from western Madagascar. Similarly, the record of *M. granulatus* from Antsingy (BLOMMERS-SCHLÖSSER & BLANC, 1991) is in need of confirmation as we did not find any voucher specimen in the MNHN and ZMA collections on which the distribution data of these authors were largely based. EMANUELI & JESU (1995) did not record *M. granulatus* from this area. The only records of the whole *Gephyromantis-Laurentomantis-Phylacomantis* assemblage occurring in western Madagascar refer therefore to *M. corvus* and possibly *M. pseudoasper*. This pattern correlates with reproductive modes. *M. corvus* and *M. pseudoasper* have tadpoles developing normally in brooks (though of derived morphology, see GLAW & VENCES, 1994); *Gephyromantis* have direct development (BLOMMERS-SCHLÖSSER, 1979; GLAW & VENCES, 1994); direct development is also probable in some *Laurentomantis* (GLAW & VENCES, 1994); and the species of the *M. granulatus* group may have either direct development (e.g. *M. leucomaculatus*) or non-feeding tadpoles (*M. granulatus*), although no detailed observations have so far been published. The absence of species with direct development and similarly derived reproductive modes from western Madagascar is probably a consequence of the need of continuous humidity for the development of terrestrial nests. The seasonal environments in western Madagascar possibly do not provide the climatic continuity for successful reproduction of direct-developing in anurans or for the survival of their diminutive juveniles. This may also be the reason for the absence of cophyline microhylids of the genus *Plethodontohyla* (with non-feeding tadpoles developing in terrestrial nests) from western Madagascar.

In the molecular analyses, the subgenus *Gephyromantis* (including the *Mantidactylus asper* group) was a paraphyletic assemblage along the branch leading towards the subgenera *Laurentomantis* and partly *Phylacomantis* (the *M. granulatus* group), while another section of *Phylacomantis* was placed basal to all these taxa (*M. corvus* and *M. pseudoasper*). Relationships of *Laurentomantis* to *M. granulatus* were also obvious from the cladograms of RICHARDS et al. (2000). If this topology was confirmed by further molecular or morphological data, it would indicate (beside the obvious diphyly of *Phylacomantis*) that the assemblage of

direct-developing *Mantidactylus* species evolved from brook-breeding ancestors such as *M. corvus* and *M. pseudoasper*. If new field data confirm that *M. granulatus* has (possibly non-feeding) tadpoles rather than true direct development, the phylogenetic topology would furthermore suggest reversal of the reproductive mode (from direct development back to tadpoles) in this species. Such a (multiple) reversal has also been suggested for Neotropical hylid frogs of the genus *Gastrotheca* (e.g., Scanlan et al., 1980; Del Pino & Escobar, 1981; Duellman & Hillis, 1987, see also discussion in Dubois, 1987): in this genus, direct development appears to be the ancestral state, and montane species from the Andes are hypothesized to have re-acquired a free swimming tadpole stage through developmental arrest in the course of their evolution. However, some Andean species of direct development may have returned again to this reproductive mode (Duellman & Hillis 1987), which would indicate a high plasticity of this trait in this frog group. The testing of these hypotheses appears highly attractive to address general questions of amphibian evolution, and may qualify – beside *Gastrotheca* – the *Gephyromantis-Laurentomantis-Phylacomantis* lineage as a suited model group for such studies.

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Une nouvelle espèce de *Scutiger* du Bhutan, et quelques remarques sur la classification subgénérique du genre *Scutiger* (Megophryidae, Leptobrachiinae)

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A new species of the genus *Scutiger* from Bhutan is described on the basis of two specimens without precise locality. The new species is placed in the *Scutiger glandulatus* group. Within this group, it differs from *Scutiger jiulongensis* by the large size of the spines on its breast, of *Scutiger glandulatus* by its important webbing and by its flattened warts on the back, and from *Scutiger tuberculatus*, which seems to be its closest known relative, by its smaller size and the absence of spines under the arms. A tentative phylogenetic analysis of a representative set of 17 species of Megophryidae, based on 54 external morphological characters, suggests that, in the genus *Scutiger*, the subgenus *Scutiger* is paraphyletic relative to the subgenus *Aelurophryne*. As these data are only preliminary, we suggest to keep using these two subgenera for the time being. We provide new diagnoses for these two subgenera, with lists of included species-groups and species.

INTRODUCTION

Le genre *Scutiger* Theobald, 1868 (Megophryidae, Leptobrachiinae) comporte une quinzaine d'espèces connues (voir GLAW et al., 1998, et FEI, 1999) de crapauds torrenticoles, de moyenne et haute altitude, de l'Himalaya, du plateau tibétain et des montagnes de l'ouest et du centre de la Chine. Deux sous-genres peuvent être reconnus au sein de ce genre (voir p. ex. FEI et al., 1991, YE et al., 1993; DUBOIS & OHLER, 1998, FEI, 1999): *Scutiger* Theobald, 1868 et *Aelurophryne* Boulenger, 1919. Etant données leur distribution et leur mode de vie, les espèces de ce groupe sont encore mal connues, et il est probable qu'un certain nombre en restent à découvrir. C'est ce qu'illustre la présente description d'une nouvelle espèce de ce genre provenant du Bhutan, petit royaume est-himalayen où jusqu'à présent fort peu de récoltes et d'observations batrachologiques ont été effectuées. Le genre *Scutiger* n'y avait pas

encore été signalé, mais la presence de *Scutiger sikimmensis* (Blyth, 1854) dans le sud-est du Sikkim, près de la frontière du Bhutan (Dubois, 1987*a*: 20) permettait de prévoir la présence de cette espèce dans ce pays. Toutefois, les deux seuls spécimens de ce genre qui figurent dans la collection d'Amphibiens effectuée en 1972 au Bhutan par une équipe du Muséum de Bâle (voir Baroni Urbani et al., 1973) s'avèrent appartenir à une espèce distincte, et dont l'inhabituelle combinaison de caractères suscite une réflexion sur la taxinomie subgénérique actuelle de ce genre. Malheureusement, aucune information précise sur la localité de capture de ces deux spécimens n'a été enregistrée dans le catalogue du Muséum de Bâle où ces spécimens ont été déposés (Rainer Gunther, lettre à AD du 2 août 1988), si bien que la localité-type de l'espèce doit rester vague, au même titre que dans certains travaux des zoologistes des siècles passés! Toutefois cette localité se trouve nécessairement sur l'itinéraire de l'expédition de 1972 du Muséum de Bâle au Bhutan (voir Baroni Urbani et al., 1973): parcourir soigneusement cet itinéraire pourrait être une manière de retrouver cette espèce dans la nature. Après avoir repoussé pendant longtemps la description de cette nouvelle espèce dans l'espoir, jusqu'à present resté vain, que des specimens provenant de localités précises en seraient récoltés, il nous paraît utile de signaler l'existence de cette espece inhabituelle à la communauté scientifique, ce qui suscitera peut-être de nouvelles recherches batrachologiques dans ce pays mal connu à cet égard, et la redecouverte de cet animal.

Méthodes et abréviations

Afin de faciliter les comparaisons, le canevas et la numérotation des caractères de la description qui suit sont les mêmes que ceux utilisés dans un recent article portant sur la même famille des Megophryidae (Dubois & Ohler, 1998), dont nous avons également repris les abréviations désignant les mesures effectuées sur les spécimens: EL, longueur de l'œil; EN, distance entre le coin antérieur de l'œil et la narine; FL, longueur du fémur (entre l'anus et le genou); FLL, longueur de la patte anterieure (entre le coude et la base du tubercule palmaire externe); FOL, longueur du pied (entre la base du tubercule métatarsien interne et l'extrémité du quatrième orteil); HAL, longueur de la main (entre la base du tubercule palmaire externe et l'extrémité du troisième doigt); FTL, longueur du quatrième orteil; HL, longueur de la tête (entre le coin postérieur de la mâchoire et l'extrémité du museau); HW, largeur de la tête; IBE, distance entre les coins postérieurs des yeux; IFE, distance entre les coins antérieurs des yeux; IMT, longueur du tubercule metatarsien interne; IN, distance entre les narines; ITL, longueur de l'orteil interne; IUE, distance minimale entre les paupières; MBE, distance entre le coin postérieur de la mâchoire et le coin postérieur de l'œil; MFE, distance entre le coin postérieur de la mâchoire et le coin antérieur de l'œil; MN, distance entre le coin postérieur de la mâchoire et la narine; MTFF, distance entre l'incurvation maximale de la palmure entre le troisième et le quatrième orteil et l'extrémité du quatrième doigt; NS, distance entre la narine et l'extrémité du museau; SL, distance entre le coin antérieur de l'œil et l'extrémité du museau; SVL, longueur entre l'extrémité du museau et l'anus; TFL, longueur du troisième doigt; TFOL, longueur du tibia et du tarse (à partir de la base du tarse); TL, longueur de la jambe; TW, largeur de la jambe; UEW, largeur maximale de la paupière. Les mesures ont été prises par MD, soit au pied à coulisse avec une précision de 0,1 mm, soit, pour les mesures inférieures à 6 mm, au micromètre oculaire avec une précision de 0,1 mm.

L'analyse cladistique a été effectuée avec le programme PAUP (SWOFFORD, 1993) en prenant les spécimens *Scaphiopus couchii* et *Pelodytes punctatus* comme outgroups.

Les spécimens étudiés dans ce travail sont déposés dans les collections de trois muséums FMNH, Field Museum of Natural History, Chicago, USA, MNHN, Museum National d'Histoire Naturelle, Paris, France, NHMB, Naturhistorisches Museum Basel, Bâle, Suisse.

DESCRIPTION DE LA NOUVELLE ESPÈCE

Scutiger (Aelurophryne) bhutanensis sp. nov.

Holotype. – NHMB 17551, mâle adulte (SVL = 53,0 mm).

Paratype. – NHMB 17550, mâle adulte (SVL = 53,4 mm).

Localité-type Bhutan. Les deux spécimens ont été récoltés, semble-t-il dans la même localité, en 1972 le long de l'itinéraire de l'expédition zoologique au Bhutan du Museum de Bâle (voir *Introduction* ci-dessus, et BARONI URBANI et al., 1973).

Description de l'holotype - (A) Taille et aspect général (fig. 1). - (1) Taille moyenne (SVL 53,0 mm), aspect ramassé.

(B) Tête (fig. 2). - (2) Tête plutôt carrée (HW 18,9 mm; HL 18,1 mm, MN 14,7 mm; MFE 12,8 mm, MBE 6,5 mm), sans coossification (3) Museau arrondi, non protubérant, plus long (SL 12,8 mm) que le diamètre de l'œil (EL 6,5 mm). (4) Canthus rostralis peu distinct, region loréale legèrement concave (5) Espace interorbital plat, plus petit (IUE 3,7 mm) que la largeur de la paupiere (UEW 6,5 mm) et la distance internasale (IN 4,6 mm), distance entre les bords antérieurs des yeux (IFE 7,5 mm) environ la moitié de celle entre les bords postérieurs des yeux (IBE 14,5 mm) (6) Narines plus proches des yeux (EN 2,7 mm) que de l'extrémité du museau (NS 3,6 mm) (7) Forme de la pupille indistincte (8) Tympan absent (9) Ocelle pineal absent. (10) Dents vomériennes absentes. (11) Dents maxillaires absentes. (12) Langue étroite, libérée sur plus d'un tiers, avec une encoche postérieure tres réduite (13) Repli supratympanique différencié en une glande parotoïde peu épaisse.

(C) Pattes anterieures (fig. 3) - (14) Patte antérieure courte (FLL 12,3 mm), aussi longue que la main (HAL 12,8 mm). (15) Doigts courts (TFL 6,8 mm) (16) Longueur relative des doigts, par ordre croissant· I et II subégaux < IV < III (17) Extremités des doigts arrondies, non élargies, sans ventouses, et de couleur claire. (18) Doigts sans franges dermiques, palmure absente. (19) Tubercules subarticulaires absents (20) Tubercule palmaire interne arrondi, ne debordant pas sur le métacarpe; tubercule palmaire externe de taille equivalente; pas de tubercule palmaire median, de tubercules surnuméraires ni de crêtes glandulaires sous les doigts.

(D) Pattes posterieures (fig 4) (21) Jambe (TL 18,9 mm, TW 6,53 mm) à peine plus courte que la cuisse (FL 20,2 mm) et que la distance entre la base du tubercule metatarsien interne et l'extremite de l'orteil IV (FOL 20,4 mm). (22) Orteils courts, orteil IV (FTL 10,5 mm) mesurant environ la moitie de la longueur totale du tibia et du tarse (TFOL 20,3 mm). (23) Longueur relative des orteils, par ordre croissant. I < II < III et V subegaux <

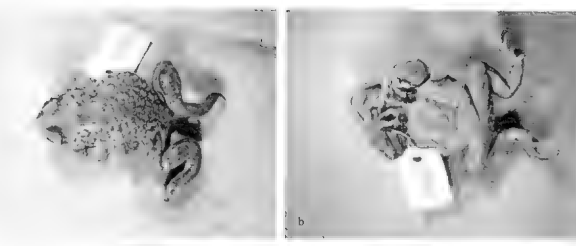




Fig. 1. – *Scutiger bhutanensis*, holotype, NHMB 17551, mâle adulte. En haut à gauche, vue dorsale; en haut à droite, vue ventrale, en bas, vue latérale

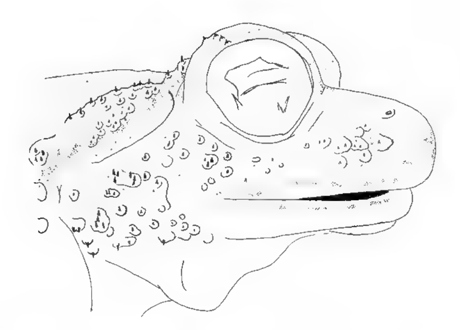


Fig. 2 - *Scutiger bhutanensis* holotype, NHMB 17551, mâle adulte. Profil du museau

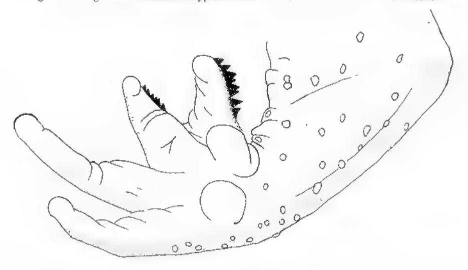


Fig. 3 *Scutiger bhutanensis*, holotype, NHMB 17551, mâle adulte. Main droite, vue de dessous.

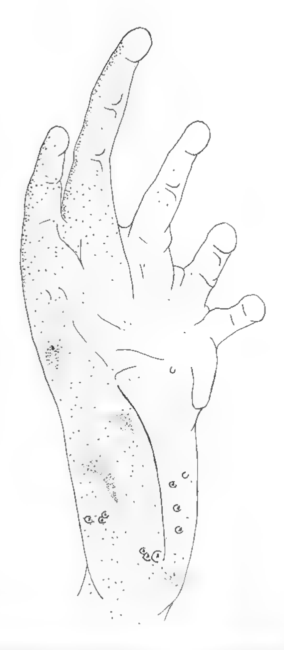


Fig. 4. – *Scutiger bhutanensis*, holotype, NHMB 17551, mâle adulte. Pied gauche, vue de dessous.

IV (24) Extrémités des orteils arrondies, non élargies et sans ventouses. (25) Palmure absente. (26) Pas de bordure dermique le long des orteils. (27) Tubercules subarticulaires indistincts. (28) Tubercule métatarsien interne distinct, plus petit (IMT 4,0 mm) que la longueur du premier orteil (ITL 3,5 mm). (29) Pli tarsien très marqué (30) Pas de tubercule métatarsien externe ni de tubercules surnuméraires.

(E) Peau. (31) Museau et zone entre les yeux à peine verruqueuse. (32) Absence de reseau sur le dos, verrues de toutes tailles couvrant le dos, petites et rondes sur les membres. (33) Pas de glandes sur le ventre, ni de lignes glandulaires latéro-ventrales. (34) Pas de macroglandes visibles extérieurement à la base des bras et sur les cuisses.

(F) Coloration en alcool (35) Taches sur le dos distribuées de façon aléatoire; trait sombre sur la tête reliant les yeux, tache importante entre les epaules. (36) Taches plutôt que bandes transversales sur les membres. (37) Anus plus foncé sans délimitation nette de coloration.

(G) Caractères sexuels secondaires mâles. – (38) Glandes axillaires, couvertes d'épines noires, situees sur les côtés de la poitrine; glandes pectorales de taille similaire, couvertes d'épines noires. (39) Coussinets nuptiaux, avec des épines épaisses, noires et très kératinisées, du bord du métacarpe jusqu'à la première articulation sur le doigt I (18 épines à droite, 17 à gauche) et tout le long du bord interne du doigt II (17 épines a droite, 16 à gauche); pas d'épines sur le doigt III. (40) Pas d'ouvertures de sacs vocaux sur les côtés du plancher buccal. (41) Épines noires, bien kératinisées, accompagnées d'aspérités, sur plusieurs parties du corps: lèvre supérieure et région loréale, très concentrées près des commissures de la lèvre inférieure, et sur la totalité du dos, cloaque inclus; épines plus fines sur les jambes et les pieds, absentes sur les bras.

Variation Les deux spécimens disponibles sont très semblables. Toutefois, les glandes porteuses d'épines sur l'ensemble du corps (dos, tempes, museau) sont moins développées chez le paratype. Chez celui-ci, les coussinets nuptiaux sont aussi moins developpés, sur le doigt I (15 épines à droite, 12 à gauche) comme sur le doigt II (14 epines à droite, 12 à gauche).

Etymologie du nom spécifique De Bhutan, nom du pays où cette espèce a été découverte

DISCUSSION

Les deux spécimens mâles étudies possedent des glandes pectorales couvertes d'épines. A haute altitude dans l'Himalaya et l'Asie centrale, parmi les Amphibiens Anoures seuls les Ranidae du genre *Paa* (tribu Paini; voir DUBOIS, 1992) et les Megophryidae des genres *Oreolalax* et *Scutiger* possèdent ce caractère (DUBOIS & OHLER, 1998, FEI, 1999) Une esquisse de phylogénie des Megophryidae, s'appuyant sur 54 caractères de morphologie externe (DELORME & DUBOIS, en préparation), suggere que ces deux derniers genres constituent un clade distinct au sein de cette famille, pour lequel nous proposons d'employer le nom tribal Oreolalagini Tian & Hu, 1985 (voir DUBOIS, 1987*b*). L'espèce nouvelle appartient sans conteste à ce dernier taxon, comme en témoignent par exemple ses glandes axillaires, ainsi que l'ensemble de sa morphologie (voir DUBOIS, 2001) Pour determiner à quel groupe au sein des

genres *Oreolalax* et *Scutiger* l'espèce nouvelle doit être attribuée, celle-ci a été comparée à divers spécimens de ces deux genres (voir app. 1).

Huit caractères de morphologie externe différents dans les deux genres excluent l'espèce nouvelle du genre *Oreolalax*: (1) étalement de la callosité nuptiale du doigt I jusqu'à la premiere articulation; (2) écart important entre les talons quand les cuisses sont disposées à angle droit par rapport au corps, (3) glandes axillaires présentes sur les côtés de la poitrine; (4) absence d'anneau tympanique; (5) replis supratympaniques en forme de glandes parotoïdes, (6) petites épines noires, très keratinisées, sur différentes parties du corps (sauf sur les coussinets nuptiaux) chez les mâles adultes; (7) absence de dents maxillaires; (8) absence de glandes fémorales visibles.

Selon Fei (1999. 339-341), les deux sous-genres du genre *Scutiger* se distinguent principalement par leurs types de caractères sexuels secondaires mâles: tandis que chez les espèces du sous-genre *Scutiger* des callosites nuptiales sont présentes sur les trois premiers doigts, dans le sous-genre *Aelurophryne* celles-ci ne sont présentes que sur les deux premiers doigts. Pour ce caractère, *Scutiger bhutanensis* correspond donc à ce dernier sous-genre. Fei (1999: 340-341) reconnaît trois groupes d'espèces dans celui-ci. Selon cet auteur, le groupe de *Scutiger gongshanensis* contient la seule espèce chinoise de ce sous-genre dont les mâles possèdent des sacs vocaux; il faut y ajouter *Scutiger adungensis* du Myanmar, dont les mâles ont de tels sacs (Dubois, 1979: 637). Le groupe de *Scutiger mammatus* se caractérise par une palmure grande ou réduite, une absence de sacs vocaux et l'absence d'epines sous les bras, comme chez l'espèce nouvelle, mais les espèces de ce groupe ne possèdent qu'une paire de plaques d'épines sur la poitrine au lieu de deux comme chez *S. bhutanensis* Enfin le groupe de *Scutiger glandulatus* réunit des especes avec ou sans palmure, sans sacs vocaux et avec deux paires de plaques d'épines sur la poitrine, mais possedant des épines sous les bras. Toutefois ce dernier caractère peut être lié à l'etat physiologique des mâles, n'étant pleinement développé que lors de la saison reproductive (Liu, 1936), et il n'est pas certain que les deux spécimens ici étudiés étaient au summum de la période reproductive, avec des caractères sexuels mâles pleinement développés. Toutefois, la présence d'épines bien noires sur la poitrine et les deux premiers doigts des deux spécimens ici décrits suggère qu'ils n'en étaient pas eloignés, et que les mâles de cette espece ne présentent jamais d'épines nuptiales sur le troisième doigt et sous les bras. Nous proposons donc de rapporter provisoirement cette espèce au groupe de *Scutiger glandulatus* Au sein de celui-ci, *S. bhutanensis* se distingue de *Scutiger jiulongensis* par la grande taille des épines sur sa poitrine, et de *Scutiger glandulatus* par sa palmure étendue et ses verrues aplaties sur le dos. *Scutiger tuberculatus* semble l'espece la plus proche de *S. bhutanensis*, dont elle se distingue notamment par la presence d'épines sous ses bras et sa grande taille (SVL des mâles adultes de 68,0 à 76,0 mm, moyenne 72 mm, Fei, communication personnelle)

L'esquisse de phylogénie des Megophryidae évoquee ci-dessus suggere un paraphylétisme du sous-genre *Scutiger* par rapport au sous-genre *Aelurophryne* (fig 5) Dans le sous-genre *Scutiger* tel que defini actuellement, plusieurs états de caractères sont inconstants, comme la presence d'épines sur le dos ou sur les bras, l'élargissement des bras des mâles par rapport a ceux des femelles et la position des glandes pectorales. Dans le passé, d'autres auteurs ont fait état d'une gradation dans la presence ou non de bourgeons de dents maxillaires au sein de ce groupe (Myers & Leviton, 1962; Inger, 1966, Anonyme, 1977;

DUBOIS, 1980, 1987*a*), ou ont retrouvé un paraphylétisme de celui-ci sur la base de caractères ostéologiques (FU et al., 1997; FU & MURPHY, 1997). Le sous-genre *Aelurophryne* constituerait un groupe mieux défini par la présence des callosités nuptiales sur le doigt I et II uniquement. Toutefois ces données ne sont encore que préliminaires et les relations phylogénétiques au sein des Megophryidae ne peuvent être tenues pour fermement établies. Pour l'instant, il nous paraît préférable de conserver les deux sous-genres, après les avoir redéfinis de manière qu'ils restent homogènes quant à la forme et la distribution des callosités nuptiales des mâles reproducteurs, caractère particulièrement frappant dans ce groupe. Pour ces raisons, nous proposons de nouvelles diagnoses pour les deux sous-genres de *Scutiger*.

La même analyse (fig. 5) suggère également un paraphylétisme du groupe de *Scutiger glandulatus* par rapport au groupe de *Scutiger mammatus*, un résultat qui devra être confirmé (ou infirmé) par une analyse phylogénétique de l'ensemble des espèces de *Scutiger*. Pour l'instant nous conservons ces deux groupes d'espèces tels qu'ils ont été définis et diagnosés par FEI (1999).

Sous-genre **Scutiger** Theobald, 1868

Espèce-type. – *Bombinator sikimmensis* Blyth, 1854, par monotypie.

Diagnose. – Ce sous-genre se distingue du sous-genre *Aelurophryne* par la combinaison suivante de caractères: (1) absence de dents maxillaires ou présence de bourgeons; (2) absence ou présence de tubercules sous-articulaires sur quelques doigts, (3) plaques pectorales des mâles de taille équivalente, ou presque, aux glandes axillaires; (4) présence de callosités nuptiales sur le doigt III des mâles; (5) épines fines et marrons sur les callosités nuptiales des mâles; (6) élargissement ou non des avant-bras des mâles; (7) présence ou non d'aspérités (selon la définition de LYNCH & DUELLMAN, 1997) sur le bord des lèvres inférieures et sur le dos des mâles; (8) absence ou présence d'épines éparses sur les bras des mâles.

Groupes d'espèces. – FEI (1999: 339-340) a défini dans ce sous-genre trois groupes d'espèces. Cette taxinomie provisoire peut être utilisée comme hypothèse de travail (voir DUBOIS, 1999: 82-84). Toutefois, afin de se conformer à la règle de priorité, qui s'applique aussi aux noms de taxons de rang infragénérique et supraspécifique tels que les groupes d'espèces (voir DUBOIS & OHLER, 1999: 137), deux de ces groupes doivent être renommés, comme ci-dessous.

Espèces incluses. – Neuf espèces, réparties comme suit dans trois groupes d'espèces: (1) groupe de *Scutiger boulengeri*: *Scutiger (Scutiger) boulengeri* (Bedriaga, 1898), *Scutiger (Scutiger) liupanensis* Huang, 1985, *Scutiger (Scutiger) ningshanensis* Fang, 1985; (2) groupe de *Scutiger chintingensis*: *Scutiger (Scutiger) chintingensis* Liu & Hu, 1960, *Scutiger (Scutiger) pingwuensis* Liu & Tian, 1978; (3) groupe de *Scutiger sikimmensis*: *Scutiger (Scutiger) maculatus* (Liu, 1950); *Scutiger (Scutiger) nepalensis* Dubois, 1974, *Scutiger (Scutiger) nyingchiensis* Fei, 1977; *Scutiger (Scutiger) sikimmensis* (Blyth, 1854).

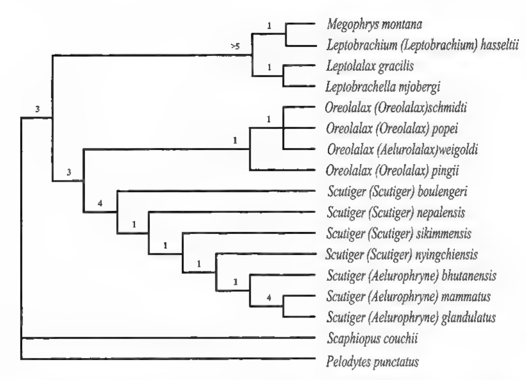


Fig. 5. - Consensus de 12 arbres equiparcimonieux de 124 pas (Delorme & Dubois, en préparation) au sein de 17 espèces de Megophryidae, basé sur 54 caractères informatifs tirés de la morphologie externe. Indice de Bremer sur les branches, CI = 0,581; RI = 0,713. Liste des caractères utilisés: (1) largeur de la tête *(aussi large que longue / plus longue que large / plus large que longue)*, (2) projection du museau en avant de la mâchoire inférieure *(absence / présence)*, (3) forme de la mâchoire inférieure *(ronde ou presque ronde / semi-circulaire avec base large / avec base allongée / avec base ronde mais extremité rétrécie)*, (4) position des narines par rapport au bout du museau et aux yeux *(à mi-distance entre les yeux et le bout du museau / plus proche du bout du museau que des yeux)*, (5) pente du museau *(profil aigu / obtus / rond)*; (6) forme du bout du museau *(bien rond / avec des arêtes ou des projections dermales)*, (7) glandes sur les paupières *(absence / presence)*, (8) forme du canthus rostralis *(très obtus avec une région loreale concave / peu distinct avec une region loreale plutôt verticale / indistinct avec une région loréale convexe)*, (9) écart entre les narines *(largement inferieur a l'espace interorbital / aussi grand que ou legèrement superieur a l'espace interobital)*, (10) tympan *(absence / presence distincte ou cachee sous la peau)*, (11) forme du repli tympanique *(fin / en forme de glande parotoïde)*, (12) glande a l'extrémite du repli tympanique *(absence / presence sous forme d'une glande rictale bien ronde / présence d'une glande en contact avec le repli supratympanique)*, (13) tache claire a l'extrémite du museau *(absence / presence)*, (14) asperites ou epines sur la lèvre superieure *(absence / presence)*, (15) aspect des epines sur l'ensemble du corps, coussinets nuptiaux exclus *(tres fines et brunes / très keratinisées et noires / tres kératinisees et noires, de très grande taille)*, (16) aspérités ou épines sur la levre inférieure *(absence / presence)*, (17) disposition des asperites sur la levre inferieure *(non regroupees / regroupees en plaques)*, (18) dents maxillaires *(absence / presence)*, (19) dents vomeriennes *(absence / presence)*, (20) liberte de la langue *(soudée, ou libre sur 1/4 maximum de sa longueur / libre sur 1/4 à 1/3 de sa longueur / libre sur plus de 2/3 de sa longueur)*, (21) crêtes pres des choanes *(absence / presence de crêtes horizontales liant les choanes / presence de crêtes retombant en arrière de la bouche)*, (22) fentes de sacs vocaux sur les côtes du plancher buccal *(absence / presence)*, (23) position et largeur des fentes des sacs vocaux *(petite ouverture, près de la commissure des levres*

Sous-genre **Aelurophryne** Boulenger, 1919

Espèce-type. – *Bufo mammatus* Günther, 1896, par monotypie.

Diagnose. – Ce sous-genre se distingue du sous-genre *Scutiger* par la combinaison suivante de caractères: (1) absence de dents maxillaires et de bourgeons; (2) présence de tubercules sous-articulaires sur tous les doigts; (3) plaques pectorales des mâles légèrement ou bien plus grandes que les glandes axillaires; (4) absence de callosités nuptiales sur le doigt III des mâles; (5) épines noires de grande taille, très kératinisées, sur les callosités nuptiales des mâles; (6) élargissement des avant-bras des mâles; (7) présence d'aspérités sur le bord des lèvres inférieures et sur le dos des mâles, (8) absence d'épines éparses sur les bras des mâles.

Groupes d'espèces. – FEI (1999: 340) a défini dans ce sous-genre trois groupes d'espèces, qui peuvent ici aussi être employés au titre de taxinomie provisoire de travail.

Espèces incluses. – Huit espèces, réparties comme suit dans trois groupes d'espèces: (1) groupe de *Scutiger glandulatus*: *Scutiger (Aelurophryne) bhutanensis* sp. nov., *Scutiger (Aelu-*

l ouverture moyenne etendue legèrement vers l avant de la bouche / grande ouverture très étendue vers l'avant de la bouche); (24) verrues dorsales *(absence / presence)*, (25) taille des verrues dorsales *(homogènes / très diverses)*, (26) aspérites sur le dos *(absence / présence)*; (27) épines dorsales *(absence / presence d'epines fines et brunes, bien definies, sur le bas du dos / présence d épines fines et brunes, bien définies, sur l'ensemble du dos)*, (28) epines cloacales *(absence / presence)*, (29) glandes laterales *(absence / presence)*; (30) position des glandes axillaires *(sur le flanc, à l insertion du bras / sur le côté de la poitrine / étendue entre l'insertion du bras et le côté de la poitrine)*, (31) taille des glandes axillaires *(aussi large que le doigt II / deux fois plus large que le doigt II)*, (32) épines sur les glandes axillaires *(absence / presence)*, (33) glandes pectorales *(absence / présence)*, (34) taille des glandes pectorales *(de taille similaire aux glandes axillaires / beaucoup plus grandes que les glandes axillaires)*, (35) écart entre les talons quand les membres postérieurs sont placés à angle droit avec le corps *(talons très écartes / talons se touchant ou se recouvrant très legèrement / talons se recouvrant très largement)*; (36) forme du tubercule palmaire externe *(allonge et diffus / rond et de la taille du tubercule palmaire interne)*, (37) tubercule palmaire médian *(absence / présence)*, (38) tubercules subarticulaires *(absence / presence sur quelques doigts / presence sur l ensemble des doigts)*, (39) crêtes sur les doigts *(absence / présence)*, (40) difference de quantite de tubercules subarticulaires entre pieds et mains *(pas de différence / présence sur les pieds mais pas sur les mains / presence sur les mains et en moindre importance sur les pieds)*, (41) verrues rondes et plates sur les bras et les mains *(absence / présence)*, (42) coussinets nuptiaux sur les doigts I et II des mâles *(absence / presence)*, (43) etalement du coussinet nuptial sur le doigt I *(etendu en arriere de la deuxième phalange du doigt I jusqu'à l'articulation entre le métacarpe et la premiere phalange / etendu en arriere de la deuxieme phalange du doigt I jusqu'a l'articulation du poignet, et même un peu au-delà)* (44) epines des coussinets nuptiaux *(très fines, à peine visibles / fines, en groupes bruns / très keratinisees, en groupes tres noirs)*, (45) coussinets nuptiaux sur le doigt III des mâles *(absence / presence)*, (46) epines regroupees en amas sous les bras *(absence / presence)* (47) epines eparses sur les bras *(absence / présence)*, (48) elargissement des bras des mâles par rapport aux femelles *(absence / presence)* (49) extension de la palmure *(orteils libres ou legere palmure au niveau des premieres phalanges / palmure large, étendue à toutes les phalanges / palmure etendue en diagonale jusqu'à la deuxieme phalange)*, (50) epines sur les pieds *(absence / presence)*, (51) glandes femorales *(non individualisees sur la cuisse / individualisees)*, (52) coloration des membres *(en bandes / diffuse)*, (53) coloration de l'anus *(absence / presence)*, (54) longueur museau anus *(inferieure a 25 mm / entre 25 et 60 mm / superieure à 60 mm)*.

rophryne) glandulatus (Liu, 1950), *Scutiger (Aelurophryne) jiulongensis* Fei, Ye & Jiang, 1999, *Scutiger (Aelurophryne) tuberculatus* Liu & Fei, 1979, (2) groupe de *Scutiger gongshanensis*: *Scutiger (Aelurophryne) adungensis* Dubois, 1979; *Scutiger (Aelurophryne) gongshanensis* Yang & Su, 1979; (3) groupe de *Scutiger mammatus*: *Scutiger (Aelurophryne) mammatus* (Günther, 1896); *Scutiger (Aelurophryne) muliensis* Fei & Ye, 1986

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Appendice I
Autres spécimens examinés

Leptobrachella mjobergi Smith, 1925. – Malaisie: *Sarawak*: 7[th] division (FMNH 222727, 222751, 222763-73, 222806).

Leptobrachium hasseltii Tschudi, 1838. – Philippines: *Mindanao* (FMNH 14893, 50919-23); *Palawan* (FMNH 51027-29).

Leptolalax gracilis (Günther, 1872). – Malaisie: *Sabah*: Kina Balu (MNHN 1898.284-287); *Sarawak*: 7[th] division (FMNH 5641, 9170, 12542, 13819, 222663-687).

Megophrys montana Kuhl & Van Hasselt, 1822. – Indonésie: *Java* (MNHN 1211). Philippines: *Mindanao* (MNHN 4537); *Palawan* (MNHN 1881.102-103, 1889.350-352).

Oreolalax (Aelurolalax) weigoldi (Vogt, 1924). – Données tirées de Ohler & Dubois (1992).

Oreolalax (Oreolalax) pingii (Liu, 1943). – Chine: *Sichuan* (FMNH 232922-29).

Oreolalax (Oreolalax) popei (Liu, 1947). – Chine: *Sichuan* (FMNH 232953).

Oreolalax (Oreolalax) schmidti (Liu, 1947). – Chine: *Sichuan* (FMNH 232938-944), Emei Shan (MNHN 1987.3854).

Pelodytes punctatus (Daudin, 1802). – France: Indre (MNHN 6465-6468, 1980.1785-1787).

Scaphiopus couchii Baird, 1854. – Mexique (MNHN 1897.398); *Baja California* (MNHN 1984.148-150); *Coahuila*: au nord de Torreon (MNHN 2152).

Scutiger (Aelurophryne) glandulatus (Liu, 1950). – Données tirées de Liu (1950).

Scutiger (Aelurophryne) mammatus (Günther, 1896). – Chine: *Sichuan*: Hlagong, près de Yajiang, à l'ouest de Kangding (MNHN 1987.3852-3853).

Scutiger (Scutiger) boulengeri (Bedriaga, 1898). – Népal: Muktinath (MNHN 1977.1146-1155).

Scutiger (Scutiger) nepalensis Dubois, 1974. – Népal: Khaptar, 2950 m, entre Doti et Chainpur (MNHN 1974.1095-1098, 1989.3361-3362).

Scutiger (Scutiger) nyingchiensis Fei, 1977. – Inde: *Jammu & Kashmir*: Shukdhari, 2920-2940 m, au-dessus de Sonamarg (MNHN 1977.1070-1128).

Scutiger (Scutiger) sikimmensis (Blyth, 1854). – Népal: Pungotanga (MNHN 1977.1199-1233); Salpa Pokhari (MNHN 1977.1263-1283).

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Análisis morfométrico de *Pleurodema thaul* (Lesson, 1826) (Anura, Leptodactylidae) y algunas consideraciones acerca de su morfología esternal

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Morphometry and anatomical variability of *Pleurodema thaul* populations from Argentina and Chile were analyzed. Multivariate statistical tests were applied to 16 morphometric variables. Results indicate that the studied populations of *P. thaul* cannot be distinguished in different morphotypes, as previously proposed. Skeletal morphology of the sternum (xiphisternum) reveals that the Argentine populations of *P. thaul* have an incised sternum, as the sternum observed in chilean specimens. Our results do not allow supporting the separation of *P. thaul* in different specific entities.

Introducción

Pleurodema Tschudi, 1838 ha sido considerado el género más primitivo de los leptodactílidos de la subfamilia Leptodactylinae debido a características plesiomorfas presentes tanto en la morfología externa de adultos y larvas como en la osteología (Lynch, 1971) Las especies que integran este género poseen un tamaño mediano (30-55 mm entre hocico y cloaca), hábitos terrestres o cavadores y, la mayoria de ellas, un par de glándulas lumbares bien desarrolladas. Osteológicamente, se caracterizan por la presencia de un amplio estilo esternal óseo, fontanela frontoparietal grande y por la ausencia de osificación cuadrado-yugal en el arco maxilar (Lynch, 1971; Cei, 1980).

Actualmente, en el género *Pleurodema* se reconocen 12 especies (Frost, 1985) y persisten algunas controversias taxonómicas. Un ejemplo lo constituye *Pleurodema borellii* (Peracca, 1895), considerada por Parker (1927) dentro de la sinonimia de *Pleurodema cinerea* Cope, 1877, pero sustentada como especie distinta por Gallardo (1968) sobre la base de diferencias de tamaño, coloración y morfología del esternón Autores tales como Barrio & Rinaldi di Chieri (1970) y Mc Lister et al (1991) se inclinan a favor de tal sinonimia, mientras que Duellman & Veloso (1977) y Cei (1980), entre otros, reconocen a *P borellii* como especie válida y distinta de *P. cinerea.*

Por otro lado, *Pleurodema thaul* (Lesson, 1826), distribuida en el sur de Argentina y a lo largo de Chile, sinonimizada tiempo atrás con las poblaciones uruguayas de *Pleurodema bibroni* (ver CEI, 1962, DONOSO-BARROS, 1969), es actualmente considerada una especie válida de elevado polimorfismo (CEI & CAPURRO, 1957; CEI & ESPINA AGUILERA, 1957, CEI, 1958, 1962). Sin embargo, debido a la amplia variabilidad morfológica, observada fundamentalmente en poblaciones chilenas, han existido dudas sobre su estatus taxonómico. DUELLMAN & VELOSO (1977) señalan la posibilidad de que bajo esta entidad puedan reconocerse más de una especie.

Pleurodema thaul se distribuye en los bosques cordilleranos patagónicos de la Argentina desde el alto valle del río Neuquén, en la provincia de Neuquén, hasta la región de los lagos Menéndez y Futalaufquen, en la provincia de Chubut. En Chile se extiende desde Antofagasta y los ríos Copiapó y Huasco, al norte, hasta la región de Aisén al sur (CEI, 1962; VELOSO & NAVARRO, 1988), ocupando ambientes tan variados como son las regiones desérticas del norte, los bosques de la región central, la selva valdiviana, las zonas cordilleranas (hasta los 1500 m) y las orillas rocosas del mar (CEI, 1958).

CEI (1958, 1962) considera que la amplia variabilidad geográfica de *P. thaul* en caracteres morfológicos, fisiológicos y etológicos tales como la longitud total, el tamaño de las glándulas lumbares, la coloración, las secreciones cutáneas y el número de relieves glandulares, representaría un polimorfismo, debido, en parte, a que algunos de estos caracteres presentan evidentes variaciones clinales a lo largo de Chile. Además, según CEI (1960), las poblaciones chilenas del norte (Copiapó, Huasco) y del sur (Llanquihue, Aisén), fenotípicamente diferentes, estarían conectadas genéticamente a través de las poblaciones intermedias y no constituirían especies o subespecies distintas. Las poblaciones argentinas de *P. thaul*, escasamente estudiadas, serían para CEI (1960) comparables a las de la región valdiviana de Chile.

DUELLMAN & VELOSO (1977) describen variación entre poblaciones de *P. thaul* en caracteres morfológicos, en el modo de deposición de los huevos, el tipo de amplexo y la morfología del esternón. Basándose en esta variabilidad y en las diferencias poblacionales observadas por VELOSO et al. (1973) a nivel cariológico, proponen la existencia de tres morfotipos dentro de *P. thaul*. Según DUELLMAN & VELOSO (1977), estos morfotipos, identificados sobre la base de su distribución geográfica como *Argentina Sur*, *Chile Sur* y *Chile Central*, deberían nominarse como especies distintas. Sin embargo, estos autores se abstienen de su reconocimiento taxonómico a causa del incompleto conocimiento de los límites distribucionales y de la variabilidad intrapoblacional. El morfotipo referido a *Argentina Sur* coincide con toda la extensión de la especie en Argentina, *Chile Sur* abarca la provincia de Llanquihue, la Isla de Chiloé y la región de Aisén; y *Chile Central* se extiende desde La Serena hasta Concepción. Las poblaciones chilenas distribuidas entre Concepción y Valdivia podrían estar integradas por representantes de los morfotipos chilenos central y sur o, incluso, constituir un taxón distinto (DUELLMAN & VELOSO, 1977).

Con el objeto de analizar la variabilidad de las diferentes poblaciones actualmente referidas a *Pleurodema thaul*, identificar caracteres que permitan establecer diferencias entre las poblaciones y aportar mayor información para dilucidar su posición taxonómica, se llevó a cabo un análisis morfométrico y se realizaron observaciones comparativas de su osteología.

Materiales y métodos

Se estudiaron 301 ejemplares adultos pertenecientes a *Pleurodema thaul* que forman parte de las colecciones herpetológicas del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), del Field Museum of Natural History (FMNH), del Museo de La Plata (MLP) y del Instituto de Limnología "Dr. Raul A. Ringuelet" (ILPLA).

Sobre cada ejemplar se registraron 16 variables morfométricas exosomáticas: (1) longitud hocico-cloaca (LHC), (2) ancho de la cabeza (AC); (3) longitud de la cabeza (LC); (4) longitud de la tibia (LT), (5) longitud del pie (LP); (6) longitud del fémur (LF), (7) distancia internarial (DIN); (8) distancia interorbital (DIO); (9) longitud de la glándula lumbar (LGL), (10) ancho de la glándula lumbar (AGL), (11) distancia del ojo a la narina (ON); (12) distancia del ojo al hocico (OH); (13) longitud del párpado superior (PAR); (14) longitud del ojo (OJO); (15) longitud del tubérculo metacarpal interno (MCI); (16) longitud del tubérculo metatarsal interno (MTI).

Las medidas fueron tomadas con calibre de escala Vernier con una precisión de 0,02 mm. Se tuvieron en consideración aquellos especímenes cuya longitud hocico-cloaca superara los 21 mm, para asegurar el estudio con ejemplares que hayan alcanzado la madurez sexual (Cei, 1962). Además, para cada uno de los especímenes se determinó el sexo sobre la base de la presencia o ausencia de saco vocal

El material proviene de 52 localidades de Argentina y Chile y abarca la mayor parte de la distribución geográfica de *P thaul* Los especímenes estudiados en cada una de las localidades se encuentran en el ap.1 Para tener en cuenta los tres morfotipos propuestos por Duellman & Veloso (1977), el material se organizó, de acuerdo a su procedencia, de la siguiente manera: (1) *Argentina Sur*: incluye las 36 localidades estudiadas de Argentina (n = 198), (2) *Chile Central* abarca Coquimbo, Zapallar, Viña del Mar, Valparaíso, Santiago y Concepción (n = 40), (3) *Chile Sur*: abarca Lago Todos Los Santos, Llanquihue, Correntoso, Chamiza, Puerto Montt e Isla de Chiloe (n = 43) Las localidades de Vegas Blancas, Cordillera de Nahuelbuta, Lago Villarrica y Valdivia pertenecen a la región chilena intermedia a *Chile Sur* y *Chile Central* (n = 20).

Análisis morfométrico

Los valores de las 16 variables morfometricas obtenidos de 301 especímenes fueron analizados utilizando técnicas estadísticas multivariadas análisis de componentes principales (ACP), análisis multivariado de la varianza (MANOVA), análisis discriminante y analisis de agrupamientos.

Los analisis de componentes principales se llevaron a cabo utilizando el programa NTSYS-pc versión 1 8 (Rohlf, 1993), mientras que el MANOVA, el análisis discriminante, el analisis de agrupamientos y las pruebas de normalidad y homogeneidad de varianza-covarianza se realizaron usando el programa STATISTICA versión 5.1 (Statsoft, 1996)

Análisis de componentes principales

Se llevaron a cabo, por sexo, tres análisis de componentes principales para establecer si las variables morfométricas permiten ordenar a los especímenes de *P. thaul* en relación con su distribución geográfica. En cada uno de estos análisis se extrajeron los tres primeros componentes principales. El primer ACP se desarrolló a partir de una matriz de varianza-covarianza de los datos transformados a logaritmo natural (ACP de varianza-covarianza); esta transformación se llevó a cabo con el fin de homogeneizar la magnitud de las variables morfométricas. En un análisis de este tipo los individuos se ordenarán en función de su tamaño y forma (REYMENT et al., 1984).

El segundo análisis de componentes principales se llevó a cabo a partir de una matriz de correlación obtenida de la estandarización de las 16 variables morfométricas (ACP de correlación). A través de la estandarización todas las variables contribuyen equitativamente en el análisis, permitiendo analizar los cambios en las proporciones de las variables morfométricas. Finalmente, el tercer ACP se llevó a cabo siguiendo el método de Burnaby (ACP de Burnaby) según lo indicado por ROHLF (1993) para remover el efecto del tamaño en la ordenación de los especímenes.

Análisis multivariado de la varianza (MANOVA) y análisis discriminante

El MANOVA se realizó para poner a prueba la hipótesis de existencia de los grupos *Argentina Sur*, *Chile Sur* y *Chile Central* dentro del material estudiado. El análisis discriminante ("forward stepwise") permitió seleccionar las variables morfométricas que mejor discriminan entre los conjuntos mencionados. Se utilizaron las variables morfométricas transformadas a logaritmo natural y los supuestos estadísticos de normalidad y homocedacia se probaron mediante el test de Kolmogorov-Smirnov y el test multivariado Box M de homogeneidad de varianza-covarianza, respectivamente.

Análisis de agrupamientos

Se realizaron, por sexo, dos análisis de agrupamientos para estudiar si la similitud morfométrica de los especímenes permite establecer agrupaciones relacionadas con la distribución geográfica. En el primer análisis se utilizaron las 16 variables morfométricas estandarizadas y como medida de similitud se empleó el coeficiente de correlación de Pearson. El segundo análisis de agrupamientos se realizó con las 16 variables morfométricas transformadas a logaritmo natural y se utilizó como medida de similitud la distancia euclideana. En todos los casos se empleó la técnica de ligamiento promedio de la media aritmética no ponderada (UPGMA) (CRISCI & LÓPEZ ARMENGOL, 1983).

ANÁLISIS DEL ESQUELETO

La morfología del esqueleto se analizó mediante preparados obtenidos según el método de doble tinción y transparentado descripto por TAYLOR & VAN DYKE (1985). El procedimiento se aplicó a un total de 19 especímenes (17 de Argentina y 2 de Chile) e incluye la tinción del tejido cartilaginoso por medio de una solución de azul Alcian, la tinción del tejido óseo

utilizando una solución de rojo de alizarina y la diafanización del tejido muscular por medio de una solución de KOH o tripsina. La duración de cada paso y las concentraciones de las soluciones se ajustaron según el estado en que se encontraba el material. Para una mejor visualización del esqueleto, la conservación final de los ejemplares se realizó en glicerina al 100 %

Resultados

Análisis morfométrico

Los estadísticos descriptivos de las 16 variables morfométricas estudiadas en *Pleurodema thaul* se encuentran detallados por sexo en la tab. 1. Además, se presentan los resultados de las pruebas de igualdad de medias entre sexos, realizadas, para cada variable, mediante el test *t* de Student. Se observa que a excepción de la variable longitud del ojo, las demás variables morfométricas muestran diferencias significativas entre los sexos ($P < 0,05$). Por otro lado, la media de las variables es mayor en las hembras que en los machos, salvo en el caso de longitud del tubérculo metacarpal interno.

La variación geográfica de las poblaciones de *P. thaul* en cuanto a longitud hocico-cloaca y longitud de la glándula lumbar se visualiza en la fig 1, en donde se representan, por sexo, la media, el desvío estándar y el rango de estas variables. Las localidades se encuentran ordenadas de norte a sur tanto en Argentina como en Chile.

Análisis de componentes principales

El analisis de componentes principales de varianza-covarianza llevado a cabo con las hembras explica, a través de los tres primeros componentes principales, el 88,05 % de la variabilidad Las variables que más contribuyen a describir esta variabilidad morfométrica son. longitud de la glándula lumbar, ancho de la glándula lumbar, longitud del tubérculo metatarsal interno, longitud del tubérculo metacarpal interno y longitud hocico-cloaca En la tab. 2 se encuentran los autovalores y autovectores obtenidos. Las ordenaciones resultantes de graficar los especímenes hembra sobre los componentes 1 vs. 2, 1 vs. 3 y 2 vs. 3 se presentan en la fig. 2 Se observa una única nube de puntos dentro de la cual no es posible encontrar ningún tipo de ordenación de los especímenes relacionada con su distribución geográfica. Por otra parte, existe una amplia superposición de los conjuntos formados por los ejemplares pertenecientes a *Argentina Sur*, *Chile Central* y *Chile Sur*. El mayor número de especímenes de *Chile Sur* se ubica a altos valores del primer y segundo componentes, mientras que la mayor cantidad del material proveniente de *Chile Central* se ubica a valores bajos de estos componentes. Sin embargo, no es posible establecer diferencias morfométricas entre estos grupos debido a su amplia superposición Los ejemplares de la región chilena intermedia (Vegas Blancas, Cordillera de Nahuelbuta y Valdivia) se agrupan tanto con los ejemplares de *Chile Central* como con los de *Chile Sur* Los ejemplares de Argentina se encuentran dispersos en la nube de puntos y superpuestos con los ejemplares chilenos, a lo largo de los tres componentes.

Tabla 1. – Estadísticos descriptivos de las variables morfométricas estudiadas en *Pleurodema thaul* por sexo (H, hembras, $n = 172$; M, machos, $n = 129$). C.V., coeficiente de variación.

Variable	Sexo	Media	Desvío estándar	Mínimo	Máximo	C.V.	Test t
Longitud hocico-cloaca	H	38.82	7.36	21.74	54.25	0.19	6.19
	M	34.32	4.27	25.80	47.44	0.12	$P < 0.05$
Ancho de la cabeza	H	13.04	2.32	6.92	18.22	0.18	4.46
	M	12.01	1.44	8.92	16.65	0.12	$P < 0.05$
Longitud de la cabeza	H	11.39	1.99	6.03	15.50	0.17	3.93
	M	10.55	1.57	7.46	19.95	0.15	$P < 0.05$
Longitud de la tibia	H	16.98	3.00	10.38	22.30	0.18	4.97
	M	15.49	1.86	10.90	22.06	0.12	$P < 0.05$
Longitud del pie	H	27.55	5.19	15.72	37.76	0.19	4.79
	M	25.08	3.15	18.10	33.10	0.13	$P < 0.05$
Longitud del fémur	H	15.53	3.16	8.68	23.48	0.20	4.84
	M	13.98	2.06	9.86	19.55	0.15	$P < 0.05$
Distancia internarial	H	2.68	0.42	1.65	3.90	0.16	6.81
	M	2.40	0.24	1.76	3.00	0.10	$P < 0.05$
Distancia interorbital	H	5.96	0.96	3.45	8.48	0.16	6.59
	M	5.34	0.53	4.35	7.86	0.10	$P < 0.05$
Longitud de la glándula lumbar	H	5.64	1.42	2.55	9.40	0.25	6.02
	M	4.76	0.97	2.95	7.84	0.20	$P < 0.05$
Ancho de la glandula lumbar	H	3.05	0.80	1.19	5.40	0.26	5.84
	M	2.56	0.60	1.40	4.30	0.24	$P < 0.05$
Distancia ojo-narina	H	3.00	0.48	1.82	4.60	0.16	5.95
	M	2.72	0.30	2.05	3.60	0.11	$P < 0.05$
Distancia ojo-hocico	H	5.42	0.90	3.25	7.40	0.17	5.86
	M	4.89	0.55	3.65	6.80	0.11	$P < 0.05$
Longitud del párpado superior	H	5.12	0.88	2.97	7.15	0.17	3.18
	M	4.84	0.61	3.70	7.05	0.13	$P < 0.05$
Longitud del ojo	H	3.92	0.65	2.29	5.40	0.17	1.81
	M	3.79	0.49	2.62	5.14	0.13	$P > 0.05$
Longitud del tubérculo metacarpal interno	H	2.14	0.50	1.20	3.95	0.23	−3.52
	M	2.32	0.36	1.40	3.10	0.16	$P < 0.05$
Longitud del tubérculo metatarsal interno	H	2.02	0.46	0.90	3.05	0.23	5.68
	M	1.75	0.36	0.70	2.90	0.21	$P < 0.05$

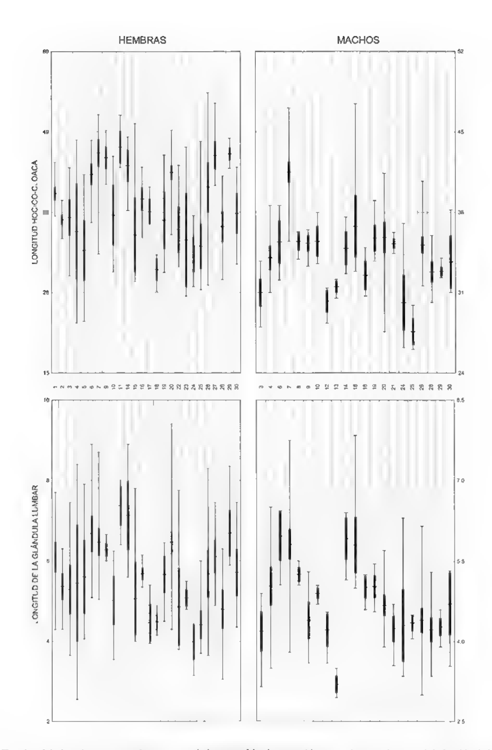


Fig. 1 Media, desvio estandar y rango de las variables longitud hocico-cloaca y longitud de la glándula lumbar, por sexo, para cada una de las siguientes localidades estudiadas (1) Coquimbo, (2) Valparaiso, (3) Santiago (4) Concepcion, (5) Vegas Blancas, (6) Valdivia; (7) Llanquihue; (8) Chamiza, (9) Puerto Montt, (10) Isla de Chiloé; (11) Alumine, (12) Lago Tromen; (13) Lago Currhue, (14) Junin de los Andes, (15) Lago Lacar, (16) San Martin de los Andes, (17) Pichi Traful; (18) Rio Pichi Traful, (19) Isla Victoria, (20) Puerto Blest, (21) Lago Frias, (22) Lago Nahue. Huapi, (23) Monte Tronador, (24) Rio Manso Superior, (25) Lago Hess, (26) El Bolsón, (27) Lago Puelo, (28) Cerro Puntudo; (29) Lago Verde, (30) Lago Futalaufquen

Tabla 2. Resultados de los tres análisis de componentes principales realizados con las hembras. Se muestran los autovectores, los autovalores y el porcentaje de varianza explicada.

Variable	ACP varianza-covarianza			ACP correlación			ACP Burnaby		
	C 1	C 2	C 3	C 1	C 2	C 3	C 1	C 2	C 3
LHC	0.196	0.002	0.023	0.977	0.025	0.068	0.836	0.376	0.303
AC	0.181	0.006	0.029	0.963	0.019	0.105	0.131	0.049	−0.185
LC	0.175	0.016	0.024	0.944	−0.045	0.103	0.072	−0.069	−0.250
LT	0.179	0.021	0.023	0.967	−0.086	0.070	0.164	−0.097	−0.257
LP	0.187	0.025	0.026	0.950	−0.102	0.077	−1.316	0.209	0.055
LF	0.191	0.019	0.035	0.895	−0.051	0.083	0.071	−1.322	0.038
DIN	0.136	−0.010	0.006	0.835	0.194	−0.041	0.027	0.049	−0.033
DIO	0.156	0.008	0.000	0.940	−0.007	−0.062	−0.007	0.062	−0.079
LGL	0.227	−0.085	−0.039	0.824	0.378	−0.112	0.240	0.146	−0.662
AGL	0.225	−0.130	−0.017	0.793	0.490	−0.127	0.175	0.035	−0.153
ON	0.132	0.014	0.015	0.817	−0.050	0.022	−0.016	−0.019	−0.036
OH	0.157	0.012	0.025	0.912	−0.015	0.134	0.021	−0.066	−0.004
PAR	0.160	0.023	0.006	0.908	−0.160	0.036	−0.029	0.090	−0.008
OJO	0.146	0.017	0.036	0.849	−0.105	0.284	−0.018	0.072	0.004
MCI	0.185	0.063	−0.105	0.793	−0.276	−0.479	−0.034	0.007	−0.040
MTI	0.208	0.051	−0.050	0.866	−0.141	−0.264	−0.006	−0.019	−0.019
Autovalor	0.517	0.034	0.022	12.725	0.579	0.478	2.577	1.997	0.731
Varianza	79.46	5.22	3.37	79.53	3.62	2.99	33.39	25.88	9.48
Acumulado	79.46	84.68	88.05	79.53	83.15	86.14	33.39	59.27	68.75

El ACP de varianza-covarianza llevado a cabo con los machos explica el 75,91 % de la variabilidad morfométrica a través de los tres componentes obtenidos. Al igual que en el análisis de las hembras las variables que más contribuyen a explicar la variabilidad son: ancho de la glándula lumbar, longitud de la glándula lumbar, longitud del tubérculo metatarsal interno y longitud del tubérculo metacarpal interno (tab. 3). Las ordenaciones de los ejemplares que se obtienen a través de los componentes principales, comparadas con las ordenaciones del análisis anterior, muestran una mayor superposición de los conjuntos formados por los ejemplares pertenecientes a *Argentina Sur*, *Chile Central* y *Chile Sur*, por lo tanto, no es posible establecer diferencias morfométricas entre estos grupos.

Los ejemplares de Argentina pertenecientes a una misma localidad están ampliamente distribuidos en la nube de puntos y superpuestos con ejemplares de otras localidades, de manera que no es posible establecer diferencias morfométricas entre las poblaciones argentinas de *P. thaul*. Estas ordenaciones se obtienen tanto al considerar a las hembras como a los machos.

En el análisis de componentes principales de correlación realizado con las hembras los tres componentes principales extraídos explican el 86,14 % de la variabilidad morfométrica. Las variables que más contribuyen a estos componentes son: longitud hocico-cloaca, longitud

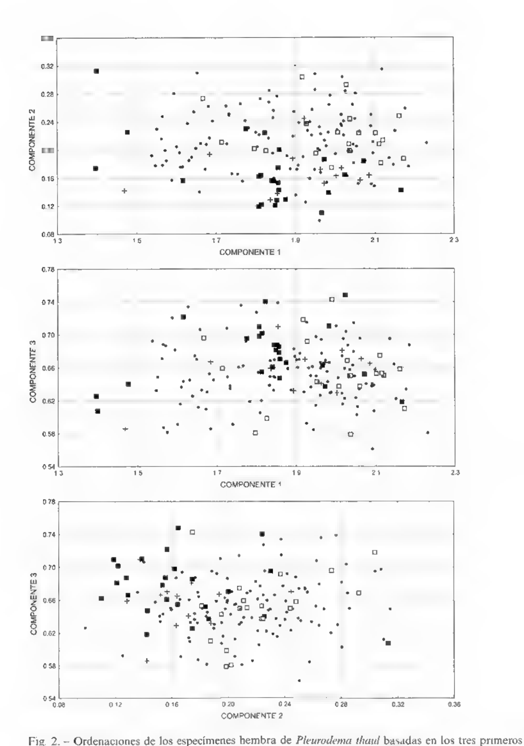


Fig. 2. – Ordenaciones de los especímenes hembra de *Pleurodema thaul* basadas en los tres primeros componentes principales del ACP de varianza-covarianza. (■) *Chile Central*, (□) *Chile Sur*, (●) *Argentina Sur*, (+) localidades de la region intermedia a *Chile Central* y *Chile Sur*

Tabla 3. Resultados de los tres análisis de componentes principales realizados con los machos. Se muestran los autovectores, los autovalores y el porcentaje de varianza explicada.

Variable	ACP varianza-covarianza			ACP correlación			ACP Burnaby		
	C 1	C 2	C 3	C 1	C 2	C 3	C 1	C 2	C 3
LHC	0.111	0.016	0.018	0.937	0.032	0.116	0.910	0.184	0.149
AC	0.106	0.020	0.017	0.920	0.021	0.026	0.132	−0.228	−0.102
LC	0.114	0.016	0.014	0.813	−0.043	0.148	0.419	−0.339	0.167
LT	0.102	0.023	0.023	0.881	0.060	−0.089	−0.178	−0.056	−0.836
LP	0.100	0.038	0.032	0.855	0.192	−0.186	−1.109	0.677	0.170
LF	0.115	0.020	0.024	0.781	−0.057	−0.308	−0.771	−1.036	0.175
DIN	0.066	0.021	0.028	0.706	0.204	−0.058	−0.025	−0.016	0.004
DIO	0.074	0.011	0.012	0.812	0.020	0.139	0.068	−0.034	−0.056
LGL	0.149	−0.102	0.025	0.664	−0.580	0.169	0.137	−0.286	−0.049
AGL	0.174	−0.136	−0.037	0.646	−0.579	0.327	0.157	−0.155	−0.062
ON	0.073	0.013	0.013	0.715	−0.115	−0.269	−0.015	−0.011	−0.052
OH	0.081	0.010	0.005	0.709	−0.183	−0.378	−0.058	−0.081	0.010
PAR	0.089	0.024	0.010	0.746	0.250	0.418	0.115	0.042	0.021
OJO	0.082	0.042	0.037	0.694	0.445	0.293	0.025	0.071	−0.016
MCI	0.116	0.048	0.005	0.725	0.199	−0.097	−0.030	−0.024	−0.035
MTI	0.149	0.065	−0.130	0.665	−0.025	−0.232	0.005	−0.031	−0.004
Autovalor	0.195	0.042	0.024	9.540	1.108	0.870	2.945	1.858	0.833
Varianza	56.66	12.18	7.07	59.62	6.92	5.44	35.93	22.66	10.16
Acumulado	56.66	68.84	75.91	59.62	66.55	71.99	35.93	58.59	68.75

de la tibia, ancho de la glándula lumbar, longitud de la glándula lumbar y longitud del tubérculo metacarpal interno (tab. 2). A partir de las ordenaciones de este análisis, al igual que en el ACP de varianza-covarianza, se observa una única nube de puntos dentro de la cual no es posible encontrar una ordenación relacionada con la distribución geográfica. Se observa una amplia superposición de los ejemplares pertenecientes a *Argentina Sur*, *Chile Central* y *Chile Sur* y por lo tanto, no es posible establecer diferencias morfométricas entre ellos. La mayor parte de los ejemplares de la región intermedia (Vegas Blancas, Cordillera de Nahuelbuta y Valdivia) se superponen con los de *Chile Central*. En la fig. 3 se representan los componentes 2 vs. 3 de este análisis.

En el ACP de correlación realizado con los machos los tres primeros componentes principales extraídos explican el 71,98 % de la variabilidad. Los resultados son similares al análisis realizado con las hembras en cuanto a las variables de mayor peso en los componentes (tab. 3) y en cuanto a la considerable superposición entre los grupos (fig. 3). En este caso, los ejemplares de Valdivia, Vegas Blancas, Cordillera de Nahuelbuta y Lago Villarrica se encuentran superpuestos tanto con los especímenes de *Chile Central* como con los de *Chile Sur*.

El análisis de componentes principales siguiendo el método de Burnaby explica, mediante los tres componentes extraídos, un porcentaje de varianza del 68,75 %, tanto si el

análisis incluye a las hembras como a los machos. En el ACP de Burnaby realizado con las hembras las variables de mayor peso son: longitud del pie, longitud hocico-cloaca, longitud de la glándula lumbar, longitud del fémur y longitud de la tibia (tab. 2) mientras que en el ACP de Burnaby realizado con los machos las variables son: longitud del pie, longitud hocico-cloaca, longitud del fémur, longitud de la cabeza y longitud de la tibia (tab. 3). Las ordenaciones que resultan de graficar los componentes 1 vs. 2 de los ACP de Burnaby de hembras y de machos se representan en la fig. 4. En ninguno de estos análisis es posible establecer diferencias morfométricas entre los grupos *Argentina Sur*, *Chile Central* y *Chile Sur*. La superposición de las nubes de puntos correspondientes a estos grupos es mucho mayor que en las ordenaciones obtenidas por ACP de varianza-covarianza y ACP de correlación. Además, no es posible encontrar ninguna otra ordenación de los ejemplares que se relacione con su distribución geográfica.

MANOVA y análisis discriminante

Se puso a prueba mediante MANOVA la hipótesis que considera a los grupos *Argentina Sur*, *Chile Central* y *Chile Sur* como entidades diferentes. Utilizando los datos morfométricos de los machos, el MANOVA llevado a cabo detectó diferencias significativas entre los grupos (Wilks' $\lambda = 0.6507$, $P < 0.05$). Las variables que mejor discriminan entre *Argentina Sur*, *Chile Central* y *Chile Sur* son longitud de la cabeza, ancho de la cabeza, longitud del tubérculo metacarpal interno y distancia del ojo al hocico. Por otro lado, utilizando una función discriminante basada en estas variables, los porcentajes de especímenes correctamente clasificados fueron 61 % para *Argentina Sur*, 67 % para *Chile Central* y 69 % para *Chile Sur*. Con las hembras se obtuvieron resultados similares.

Análisis de agrupamientos

Los análisis de agrupamientos realizados, tanto con las hembras como con los machos, no permitieron la agrupación de los especímenes según un patrón de distribución geográfica. Los diversos agrupamientos formados contienen representantes de localidades muy variadas, provenientes tanto de *Argentina Sur* como de *Chile Central* o *Chile Sur*. En todos los casos, los especímenes procedentes de Argentina se agrupan con especímenes de Chile. Con respecto a las localidades argentinas, tampoco es posible encontrar agrupaciones que se relacionen con su distribución geográfica; especímenes del norte de Argentina (Caviahue, Lago Tromen) se agrupan con aquellos del centro (Puerto Blest) y sur (Lago Futalaufquen). Los resultados del análisis de agrupamientos empleando el coeficiente de correlación de Pearson se presentan, para los machos, en la fig. 5.

Análisis del esqueleto

Las observaciones realizadas sobre los distintos constituyentes del esqueleto de *Pleurodema thaul* no permitieron encontrar diferencias morfológicas de relevancia en el material estudiado. Los datos obtenidos más importantes se refieren a la morfología de la porción posterior del esternón (xiphisternón), de estructura cartilaginosa.

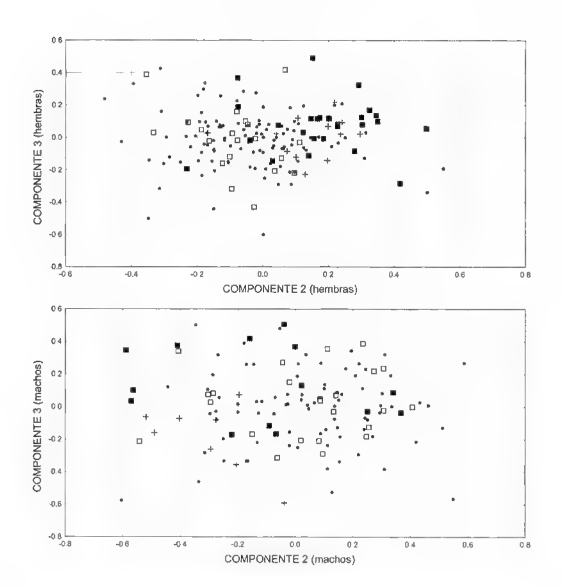


Fig. 3. – Ordenación de especímenes de *Pleurodema thaul* basada en los componentes principales 2 y 3 del ACP de correlación para hembras y machos. (■) *Chile Central*, (□) *Chile Sur*, (●) *Argentina Sur*, (+) localidades de la región intermedia a *Chile Central* y *Chile Sur*.

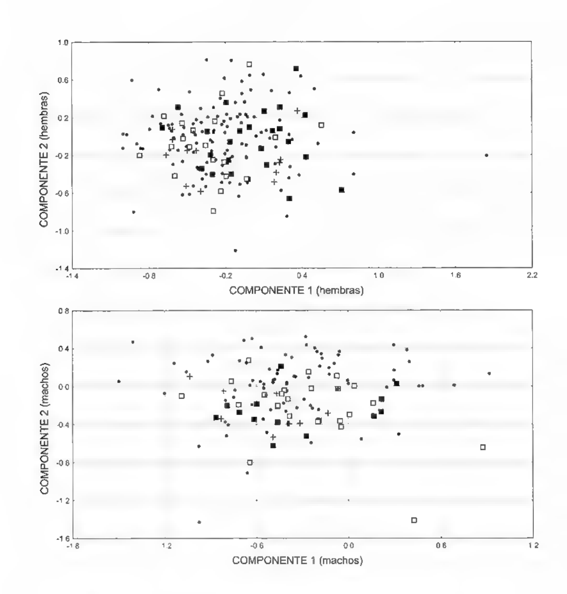


Fig 4. Ordenación de especímenes de *Pleurodema thaul* resultante de los componentes principales 1 y 2 del ACP de Burnaby para hembras y machos. (■) *Chile Central*, (□) *Chile Sur*, (●) *Argentina Sur*, (+) localidades de la región intermedia a *Chile Central* y *Chile Sur*.

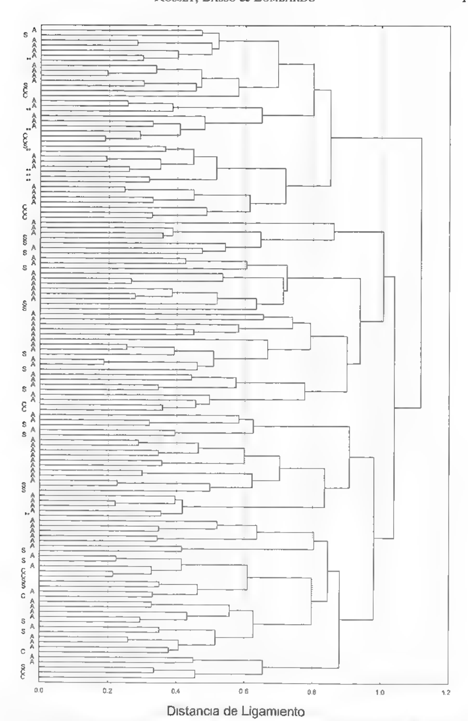


Fig 5 Fenograma obtenido del análisis de agrupamientos de los machos, utilizando el coeficiente de correlación de Pearson y la técnica de ligamiento promedio de la media aritmética no ponderada. C. *Chile Central*; S. *Chile Sur*; A. *Argentina Sur*; ** localidades chilenas intermedias.

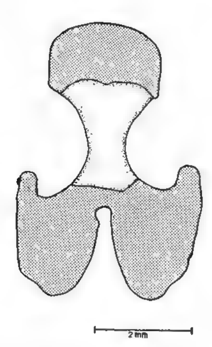


Fig. 6 - Esternon de *Pleurodema thaul* (ILPLA A 490, macho), Lago Futalaufquen, Chubut, Argentina.

En la totalidad de los especímenes examinados (9 hembras y 10 machos), pudo visualizarse claramente la presencia de un xiphisternón inciso posteriormente, tanto para los especímenes de Chile como para los de Argentina (fig. 6)

Discusión y conclusiones

A través de análisis de componentes principales, utilizando 16 variables morfométricas, se obtuvieron ordenaciones de especímenes de *Pleurodema thaul* basadas en la variabilidad de tamaño y forma (ACP de varianza-covarianza), en las proporciones entre las variables (ACP de correlación) y en la variabilidad en forma (ACP de Burnaby).

En los tres casos, estas ordenaciones constituyen un único conjunto de ejemplares dentro del cual no es posible encontrar diferencias morfométricas entre las poblaciones estudiadas que se correspondan con la distribución geográfica. En la mayor parte de los casos, la distancia morfométrica entre ejemplares pertenecientes a una misma localidad es mayor que aquella entre ejemplares pertenecientes a distintas localidades, lo cual no permite establecer diferencias en la morfometría de las poblaciones.

Por otro lado, tampoco es posible establecer diferencias morfométricas entre las poblaciones asignadas a *Argentina Sur*, *Chile Central* y *Chile Sur*, que resultan de agrupar las localidades de colecta del material teniendo en cuenta las consideraciones taxonómicas realizadas por Duellman & Veloso (1977).

A través de MANOVA y análisis discriminante, se puso a prueba la hipótesis de que los morfotipos referidos a *Argentina Sur*, *Chile Central* y *Chile Sur* representan entidades morfométricamente distintas. Los resultados de estos análisis muestran que no es posible diferenciar a través de la morfometría estas tres agrupaciones geográficas de *P. thaul*. Aunque con MANOVA se detectan diferencias estadísticamente significativas, la correcta clasificación de los especímenes en estos grupos involucra un porcentaje de error muy alto (31-39 %) como para establecer diferencias morfométricas significativas entre ellos.

Los análisis de agrupamientos presentan resultados similares en cuanto a que no se ha podido establecer una correspondencia entre los grupos obtenidos del análisis y la distribución geográfica

En este trabajo no ha sido posible el estudio de especímenes de *P thaul* provenientes de las poblaciones del norte de Chile (Antofagasta, Río Copiapó, Río Huasco). DUELLMAN & VELOSO (1977) señalan la existencia de una población en el desierto de Pajonales (al norte de la provincia de Coquimbo) que podría representar un taxón distinto. NORTHLAND et al. (1996) muestran que las poblaciones de Antofagasta son morfométricamente más similares a las de la zona central de Chile que a las de Copiapó, geográficamente más cercanas.

DUELLMAN & VELOSO (1977) utilizan la ausencia de incisión esternal como el caracter más importante para diferenciar las poblaciones distribuidas en Argentina de las poblaciones chilenas de *P thaul* Estos autores atribuyen a las poblaciones argentinas un xiphisternón redondeado posteriormente, mientras que las poblaciones atribuidas a Chile presentan el xiphisternón hendido. A través del estudio detallado de la morfología del esternón se observó que todos los especímenes estudiados, tanto de Argentina como de Chile, poseen el xiphisternón hendido.

Los resultados morfometricos obtenidos en este trabajo, junto con los datos provenientes de la morfología del esternón, no permiten identificar caracteres para establecer diferencias entre las poblaciones estudiadas de *P. thaul*.

RESUMEN

Se analiza la variabilidad morfométrica y anatomica de poblaciones argentinas y chilenas del *Pleurodema thaul*. Se aplicaron métodos estadísticos multivariados sobre un total de 16 variables morfométricas. Los resultados indican que las poblaciones estudiadas de *P. thaul* no pueden ser diferenciadas en morfotipos distintos, según ha sido propuesto en trabajos previos. El estudio morfológico del esqueleto revela que el esternón (xiphisternón) de las poblaciones argentinas de *P thaul* presenta una incisión en su porción posterior, similar a la observada en las poblaciones chilenas. Estos resultados no permiten sustentar la propuesta de separar a *P thaul* en entidades específicas distintas.

Agradecimientos

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APÉNDICE I

Material examinado

Los especímenes resaltados en negritas corresponden a ejemplares diafanizados y teñidos para estudio de su esqueleto.

ARGENTINA (n = 198: 115 ♂ y 83 ♀). (1) Caviahue, 2 ♀, MACN 27613-4; (2) Laguna Blanca, 1 ♀, MACN (ex CENAI) 8786; (3) Lago Nompehuen, 1 ♀, ILPLA A.483, (4) Aluminé, 3 ♀, **MACN 11648-9**, 11650; (5) Lago Tromen, 1 ♀ y 3 ♂, MACN (ex CENAI) 932-4, 937; (6) Lago Epulafquen, 1 ♂, **ILPLA A.487**; (7) Laguna Verde, 1 ♀, ILPLA A.480; (8) Lago Curruhue, 2 ♀ y 3 ♂, MACN (ex CENAI) 2014-6, 2170-1, (9) Junín de los Andes, 4 ♀ y 3 ♂, **MACN 28703**, 28704-6, 32117, **32118**, 32120; (10) Lago Lácar, 4 ♀, MACN (ex CENAI) 9146, 9149-50, MACN 36072; (11) San Martín de los Andes, 5 ♀ y 5 ♂, MACN (ex CENAI) 5986-90, MACN 11867-70, **ILPLA A.489**, (12) Pichi Traful, 3 ♀ y 1 ♂, MACN (ex CENAI) 1878-81; (13) Río Pichi Traful, 3 ♀ y 3 ♂, MACN (ex CENAI) 901, 903-7; (14) Lago Espejo, 2 ♂, MACN (ex CENAI) 1052-3, (15) Isla Victoria, 4 ♀ y 4 ♂, MACN (ex CENAI) 4090, 4094, 4097, 4099, **4107**, **MACN 9092**, MLP A 532-3, (16) Puerto Blest, 17 ♀ y 9 ♂, MACN (ex CENAI) 1527.1-3, **1527.5**, 1527.7, **1527.8**, 1527.9, 1527.11, 1527.13-16, 1527.19-20, 1956-8, 1960-3, 1967-8, 3312, MACN 31552, MLP A 425, (17) Lago Frias, 2 ♀ y 4 ♂, MACN (ex CENAI) 7151-6, (18) Lago Perito Moreno, 2 ♀ y 1 ♂, MACN (ex CENAI) 2671-3, (19) Lago Nahuel Huapi, 4 ♀ y 2 ♂, MACN (ex CENAI) 1611, 2305-7, MLP A.1079-80, (20) San Carlos de Bariloche, 2 ♂, MACN 28209-10, (21) Cerro Otto, 2 ♀, MACN 11180, MLP A.421, (22) Monte Tronador, 3 ♀, MACN (ex CENAI) 915-6, MACN 9651, (23) Cerro Catedral, 1 ♀ y 1 ♂, MACN (ex CENAI) 8801-2; (24) Cerro Challhuaco, 1 ♀ y 1 ♂, ILPLA A 481, **488**, (25) Río Manso Superior, 4 ♀ y 4 ♂, MACN (ex CENAI) 917-23, 925, (26) Río Manso, 2 ♀ y 2 ♂, MACN (ex CENAI) 4717-20; (27) Lago Hess, 6 ♀ y 3 ♂, MACN (ex CENAI) 1097-102, 1104, 1107.6, 1107.12, (28) El Foyel, 2 ♀, MACN 11435-6, (29) Rio Azul, 1 ♀, MACN 15319; (30) El Bolsón, 8 ♀ y 13 ♂, MACN (ex CENAI) 3611-6, **3617**, 3618, **3619**, 3620-6, 4577, MACN 14816-8, 15416, (31) Lago Puelo, 6 ♀ y 2 ♂, MACN 15320, 26144-50; (32) Cerro Puntudo, 7 ♀ y 7 ♂, MACN (ex CENAI) 8805-6, **8807**, 8808-9, 8811-6, **8817**, 8818-9; (33) Lago Menendez, 2 ♀, MACN (ex CENAI) 7161-2, (34) Lago Verde, 4 ♀ y 4 ♂, MACN (ex CENAI) 8820-5, **8826**, 8827, (35) Lago Futalaufquen, 5 ♀ y 3 ♂, MACN (ex CENAI) 7171-2, ILPLA A 479, 482, 484-6, **490**, (36) Lago Situación, 2 ♀, MACN 29826-7

CHILE (n = 103: 57 ♀ y 46 ♂). (1) Coquimbo, 8 ♀, FMNH 132471, 132488-9, 132508, 132518, 132531, 132778-9, (2) Zapallar, 1 ♀ y 2 ♂, MACN (ex CENAI) 1446-8, (3) Viña del Mar, 1 ♀, MACN 12409; (4) Valparaíso, 6 ♀, MACN (ex CENAI) 1620-1, FMNH 132721, 132723, 132733-4, (5) Santiago, 5 ♀ y 4 ♂, MACN (ex CENAI) 1622-4, **1625**, 1626, 8791-4; (6) Concepción, 4 ♀ y 9 ♂, MACN (ex CENAI) 4428-32, FMNH 214120, 214122, 214137-8,

214141, 214161, 214169-70; (7) Vegas Blancas, 4 ♀ y 2 ♂, MACN (ex CENAI) 1234, 1237, 1912-5, (8) Cordillera de Nahuelbuta, 1 ♀ y 1 ♂, MACN (ex CENAI) 1906-7; (9) Lago Villarrica, 2 ♂, MACN 28794-5; (10) Valdivia, 7 ♀ y 3 ♂, MACN 4639-48; (11) Lago Todos Los Santos, 1 ♀, MLP A 2143; (12) Llanquihue, 10 ♀ y 12 ♂, FMNH 212588-95, 212604-10, 212612, 212775, 212779, 212782, 212787-8, 212792, (13) Correntoso, 1 ♀ y 1 ♂, MACN (ex CENAI) 1923-4; (14) Chamiza, 3 ♂, MACN (ex CENAI) 1951, **1952**, 1953; (15) Puerto Montt, 4 ♀ y 4 ♂, MLP A.1989, 1991, 1994-5, 2000-1, 2004-5; (16) Isla de Chiloé, 4 ♀ y 3 ♂, FMNH 212596-7, 212599-602, 212613.

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Microscopía electrónica de barrido del aparato bucal y cavidad bucofaríngea de la larva de *Atelognathus nitoi* (Anura, Leptodactylidae)

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Larvae of *Atelognathus nitoi* were collected in the Province of Río Negro (Argentina). The microanatomy of the oral apparatus and of the buccopharyngeal cavity of these tadpoles is described with scanning electron microscope and observed with stereoscopic microscope. The buccal apparatus has short labial teeth formed by a short base, a short neck, and a multicusped paddle with 10-12 short denticles. The horny beak is wider than high and the teeth are unicusped. The bucopharingeal cavity has two pairs of infralabial papillae and four lingual papillae, the median ridge is triangular, the lateral ridges are simple, the ventral velum and the glandular zone are present at the posterior side. The intestinal contents consist of cysts and scales of algae (Chrysophyta, Chrysophycea), frustula of diatoms and fungi.

Introducción

Atelognathus nitoi (Barrio, 1973) es un leptodactílido microendémico de la Laguna Verde del Cerro Challhuaco (Parque Nacional Nahuel Huapi), ubicado en el noroeste de la patagonia argentina. De las ocho especies de *Atelognathus* reconocidas, hasta el presente sólo fueron descriptas las larvas de *Atelognathus patagonicus* (Gallardo, 1962) (Cei, 1965), *Atelognathus reverberii* (Cei, 1969) (Cei, 1969) y *Atelognathus nitoi* (Basso & Úbeda, 1997), y la microanatomía de la cavidad bucofaríngea de las dos primeras species fue descripta por Wassersug & Heyer (1988) La larva de *A. nitoi*, recientemente descripta (Basso & Úbeda, 1997), se desarrolla en la citada laguna y en ocasiones en ambientes temporarios cercanos. En sus primeras semanas de vida, los renacuajos habitan las playas de la laguna y muestran un hábito nadador. A medida que crecen se internan en la parte mas profunda de la laguna,

Tabla 1. Larvas de *Atelognathus nitoi*: material estudiado del Parque Nacional Nahuel Huapi, Argentina.

N° ejemplar	113	114	115	181	189	190	214	218
Estadio	31	26	31	26	27	31	27	37
Localidad (Laguna)	sin nombre	Verde	sin nombre	Verde	Verde	sin nombre	Verde	Los Patos

manteniendo el hábito nadador y frecuentando el fondo (Úbeda et al., 1999) Durante el período premetamórfico presentan un morfotipo adaptativo léntico-béntico (Basso & Úbeda, 1997)

El propósito de este trabajo es describir el aparato bucal y la cavidad bucofaríngea de *A nitoi* mediante observaciones con microscopio electrónico de barrido, discutir sus relaciones ecomorfológicas y comparar con las otras especies conocidas de *Atelognathus* y con géneros afines.

Material y métodos

Las larvas estudiadas provienen de la Laguna Verde (localidad tipo de la especie) y de ambientes acuaticos temporarios vecinos, ubicados en un bosque de lenga (*Nothofagus pumilio*) entre 1350 y 1550 m s.n.m, en el Cerro Challhuaco, Parque Nacional Nahuel Huapi, provincia de Rio Negro, Argentina Las larvas fueron capturardas con redes de mano y fijadas in toto en formol 10 %. Siete ejemplares (N°113-115, 181, 189-190 y 214, Colección Larvas DDE, para Microscopio electrónico de barrido, tab 1) corresponden a los estadios 26 al 31 de la tabla de desarrollo de Gosner (1960). Se disecó un ejemplar en estadio 37 (ejemplar N°218, lote 206, Comahue, tab. 1) para comparar el desarrollo de la papilación bucofaríngea con los estadios menores.

Las observaciones en microscopio electrónico de barrido se realizaron tratando al material según las técnicas propuestas por Wassersug (1980) y Echeverria (1995), efectuándose una deshidratación rapida en alcohol etilico (80 %, 8 h; 96 %, 2 h, 100 %, 1 h), en alcohol etílico-acetona (3:1, 1 h; 1:1, 1 h; 1:3, 10h) y en acetona pura, como máximo dos horas antes de proceder a la desecacion final Se efectuó el punto crítico de desecación en un secador al vacío Balzers 030 La metalización se realizó con oro en un metalizador ION Sputtering Balzers CPD 040. Las observaciones y fotografías se realizaron en un microscopio electrónico de barrido Philips 505 El punto crítico de desecación se efectuó en un secador al vacío Balzers CPD 030. La metalizacion se efectuó con oro en un metalizador Balzers SCD 040 Las descripciones de las formaciones corneas del aparato bucal y cavidad bucofaríngea se realizaron según la terminologia propuesta por Decneff & Beaumont (1959), Viertel (1982) y McDiarmid & Altig (1999). La fórmula dentaria se expreso siguiendo la propuesta de Dubois (1995)

El contenido intestinal de las larvas fue examinado en diferentes estadios de desarrollo (26, 27 y 31) a fin de relevar en forma cualitativa los diferentes ítems alimentarios y sus características ecológicas.

Las ilustraciones fueron realizadas con un microscopio estereoscópico Nikon SMZ 10 TD, provisto de cámara de dibujo.

RESULTADOS

APARATO BUCAL

El disco oral es emarginado y con un amplio claro rostral. Está limitado lateralmente por una hilera de papilas marginales cónicas y simples y por papilas submarginales similares, bien desarrolladas, en las regiones supraangular e infraangular (fig. 1a-b). A nivel del cartílago de Meckel pueden observarse 2 papilas angulares intramarginales bajas (fig. 1c). Las papilas mentales son cónicas, alargadas, con el extremo agudo, extendiéndose en una hilera simple (fig. 1d).

Los queratodontes forman una hilera continua y homogénea, el numero de dientes en un ejemplar correspondiente al estadio 31 es de aproximadamente 5 a 7 en 100 μm. Están formados por una base, un cuello y una espátula con 10 a 12 dentículos cortos. La longitud total de un diente labial es 25 a 30 μm, con un ancho máximo de la espátula de 15 μm (fig. 1e). Los dientes del pico córneo están organizados en empalizada, con una densidad de 5 dientes en 100 μm; presentan un largo total de aproximadamente 25 a 30 μm y un ancho máximo de 20 μm (fig. 1f).

CAVIDAD BUCOFARÍNGEA

Piso

La región prelingual presenta cuatro papilas infralabiales, dos ventrales y dos laterales. Sobre el esbozo lingual se desarrollan cuatro papilas linguales simples; las papilas centrales son más largas y mas cercanas al borde lingual anterior que las laterales (fig. 2a). La arena del piso de la cavidad oral esta limitada lateral y posteriormente por papilas periféricas bien desarrolladas. En el estadio 31 las papilas son más abundantes que en los estadios 26 y 27 (fig. 2b).

Las hendiduras bucales son alargadas y están ubicadas transversalmente con respecto a la línea media. El área lateral interna de la prehendidura está precedida por proyecciones laminares, cuyos extremos digitiformes se dirigen hacia el interior de la cavidad bucofaríngea. Estas presentan los bordes rugosos y se destacan del resto de las papilas por su mayor desarrollo. Cercanas al borde anterior de la hendidura se observan 1 a 3 papilas bajas (fig. 2b). El velo ventral tiene 4 a 5 proyecciones marginales pronunciadas y espaciadas a ambos lados de la escotadura mediana. Las proyecciones que forman la escotadura son pronunciadas y le

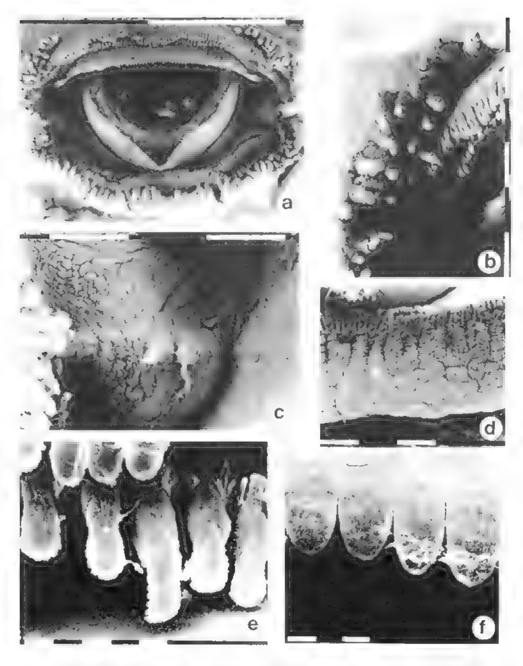


Fig. 1. Aparato bucal de *Atelognathus nitoi* (estadio 31). (a) Vista general. Escala: 1 mm. (b) Detalle de las papilas del disco oral. Escala: 0,1 mm. (c) Detalle de las papilas angulares intramarginales del disco oral. Escala: 0,1 mm. (d) Papilas mentales del disco oral. A, papilas mentales. Escala: 0,1 mm. (e) Dientes labiales en la hilera A-2. Escala: 10 µm. (f) Pico córneo. Escala: 10 µm.

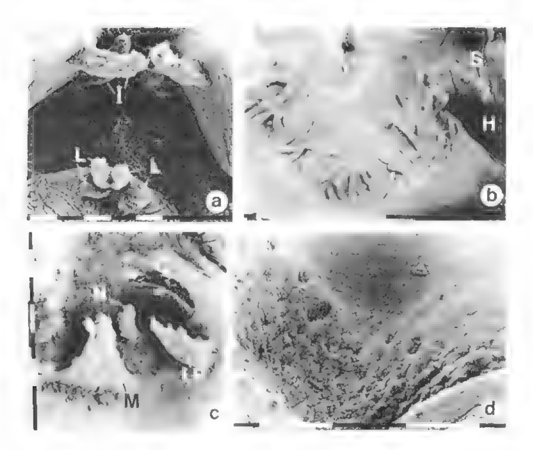


Fig 2 Cavidad bucofaríngea de *Atelognathus nitoi* (a) Piso. area prelingual I, papilas infralabiales, L, papilas linguales. Estadio 27 Escala: 0.1 mm. (b) Region posterior del piso. H, hendidura bucal derecha, P, papilas perifericas, S, tres papilas en el borde anterior de H Estadio 31. Escala 1 mm (c) Techo C, coana, LP, pliegue lateral; M, pliegue mediano, N, papila postnasal. Estadio 26 Escala: 0,1 mm. (d) Region glandular posterior del techo. Estadio 31. Escala. 0,1 mm.

confieren a ésta forma de "V" El borde del velo y sus proyecciones presentan fosetas glandulares.

Cabe destacar que en un ejemplar en estadio 37 (de 73 mm de longitud total), las papilas infralabiales laterales presentaron bordes irregulares y las papilas linguales centrales se hallaron ramificadas.

Techo

Las coanas son de forma elíptica, convergentes anteromedialmente, protruyentes hacia la cavidad bucofaríngea En el área posnarial, en estadios 26 y 27, se halla un par de papilas postnasales (fig 2c) Los pliegues laterales son proyecciones simples, bien desarrolladas, con

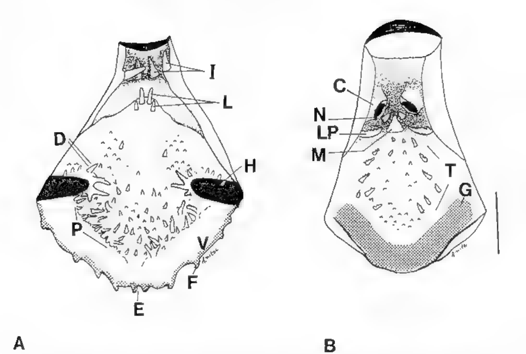


Fig. 3. – Morfología de la cavidad bucofaríngea de la larva de *Atelognathus nitoi* (estadio 31). (A) piso, (B) techo. C, coana; D, papilas prehendidura; E, escotadura mediana; F, proyección marginal; G, region glandular; H, hendidura bucal; I, papila infralabial; L, papilas linguales; LP, pliegue lateral; M, pliegue mediano; N, papila postnasal; P, papilas periféricas del área del piso de la cavidad bucofaríngea; T, papilas del margen del área del techo de la cavidad bucofaríngea; V, velo. Escala 1 mm.

forma de lámina comprimida en sentido anteroposterior, su borde ventral es irregular y el dorsal liso. El pliegue mediano tiene forma triangular, paredes lisas y bordes irregulares. Las papilas marginales de la arena del techo de la boca son escasas (de 5 a 6 pares), cónicas y altas; en la región posterior se hallan numerosas pustulas. El área glandular está muy desarrollada; se dispone en forma de banda en U abierta en los extremos; las fosetas glandulares presentan forma circular o irregular (fig. 2d). En el ejemplar 218, se hallaron dos pares de papilas postnasales de diferente tamaño, siendo el par mas externo de tamaño muy reducido.

En la figura 3 se reúnen las características típicas de la cavidad bucofaríngea de *A. nitoi* para el estadio 31.

Contenido intestinal

En dos ejemplares correspondientes a los estadios 26 y 27 (ejemplares 181 y 189), provenientes de la Laguna Verde, se hallaron quistes y escamas de algas (Chrysophyta, Chrysophycea) cuyo tamaño de partícula osciló entre 3 a 5 µm en los quistes y entre 10 a

12 µm en las espículas. Se hallaron frústulos de diatomeas (Bacillariophyceae, *Diploneis* sp., *Navicula* sp., *Cymbella* sp.) de largo máximo hasta 60 µm. Se observó, además, la presencia de hifas de hongos acuáticos (ejemplares 115, 181 y 189).

DISCUSIÓN Y CONCLUSIONES

La larva de *Atelognathus nitoi* presenta una distribución de hileras de queratodontes que responde a la fórmula 1:<1>/<1>:2, tal como fuera observado por BASSO & ÚBEDA (1997). Este tipo de distribución de los denticulos córneos es muy frecuente entre las larvas de aguas quietas (ALTIG & JOHNSTON, 1989) y es compartida por la mayoría de los leptodactílidos telmatobiinos patagónicos: *Alsodes barrioi*, *A. gargola*, *A. monticola*, *Atelognathus patagonicus*, *A. reverberii*, *Batrachyla antartandica*, *B. leptopus*, *B. taeniata*, *Caudiverbera caudiverbera* y *Hylorina sylvatica* (FORMAS & PUGÍN, 1978*a-b*; LAVILLA, 1988), con la excepción del genero *Eupsophus*, que presenta una reducción en el número de hileras de queratodontes asociada a una alimentación endotrófica (FORMAS & PUGÍN, 1978*a-b*; FORMAS, 1989*a-b*, 1992). Los queratodontes son relativamente cortos en relación con los dientes de otros leptodactílidos de ambientes lénticos conocidos, como los observados en *Odontophrynus americanus* y *Leptodactylus ocellatus* (ECHEVERRÍA & MONTANELLI, 1992; ECHEVERRÍA, 1995).

En cuanto a la papilación del disco, *A. nitoi* presenta escasas papilas suprangulares e infrangulares con una distribución irregular, y papilas mentales. Las papilas marginales mentales son alargadas y se disponen en una hilera limitando al disco por su parte posterior, confirmando lo indicado por LAVILLA (1988) para el género *Atelognathus*. El disco oral de *A. nitoi* se distingue del de *Alsodes gargola* por presentar una hilera de papilas mentales marginales, a diferencia del género *Alsodes*, que tiene dos hileras mentales, una marginal y otra intramarginal, cada una con distinta morfología (ECHEVERRÍA et al., 2001). En la zona angular intramarginal de *A. nitoi* se observan dos papilas poco desarrolladas ubicadas a nivel del cartílago de Meckel. Éstas son las únicas papilas en la zona angular que se hallan en posición intramarginal, aisladas y ubicadas más internamente que las restantes papilas submarginales.

La cavidad bucofaringea presenta características anatómicas comunes con otros leptodactílidos. *Atelognathus nitoi* comparte con las larvas de los leptodactílidos de los géneros *Alsodes*, *Atelognathus*, *Batrachyla*, *Caudiverbera*, *Hylorina*, *Pleurodema* y *Odontophrynus* (BRILVA VÁSQUEZ, 1988, WASSERSUG & HEYER, 1988) la presencia de cuatro papilas linguales y cuatro papilas infralabiales. Cabe destacar que las características atribuidas a *Eupsophus roseus* por WASSERSUG & HEYER (1988) no son consideradas en este trabajo debido a la identidad dudosa del especimen KU 162057, inferida a partir de las notas de campo sobre el hábitat, la coloracion y el tamaño del ejemplar. La morfologia de la cavidad bucofaringea de *Atelognathus nitoi* coincide con la observada en *A. patagonicus* y *A. reverberii* (WASSERSUG & HEYER, 1988) en cuanto a la presencia de cuatro papilas infralabiales, cuatro papilas linguales, un pliegue mediano triangular y pliegues laterales simples y bien desarrollados. Comparte con *Leptodactylus ocellatus* cuatro papilas linguales y la forma y textura de los bordes dorsal y ventral del pliegue lateral (ECHEVERRÍA, 1995).

Los telmatobinos patagónicos que poseen la misma fórmula dentaria que *A. nitoi* pueden hallarse en ambientes lóticos, lénticos, temporarios o permanentes. Sus características ecomorfológicas también son variadas, observándose formas bentónicas y nectónicas (Cei, 1980).

Al analizar el contenido intestinal de *A. nitoi,* se halló un rango muy amplio de ítems alimentarios (algas y hongos) con tamaños de partícula comprendidos entre 3 y 60 µm. De la observación con microscopio electrónico de barrido se amplían los ítems alimentarios previamente reportados por Úbeda et al. (1999), confirmándose la predominancia de algas planctónicas y perifíticas en el contenido intestinal de *A. nitoi.*

La morfología del aparato oral y de la cavidad bucofaríngea observada en *Atelognathus nitoi* presenta características coincidentes con las reportadas para otras especies del género *Atelognathus*. Los caracteres compartidos con otros géneros de telmatobinos patagónicos, de hábitos diferentes, deben atribuirse fundamentalmente a una restricción filogenética dada por ancestralidad común, prevaleciendo sobre las adaptaciones ecológicas convergentes.

Resumen

Se describe la microanatomía del aparato bucal y la cavidad bucofaríngea de la larva de *Atelognathus nitoi* observada con microscopio electrónico de barrido y microscopio estereoscópico sobre especímenes colectados en la provincia de Río Negro (Argentina). El aparato bucal presenta dientes labiales relativamente cortos formados por una base y cuello cortos y una espátula multicuspidada, con 10 a 12 dentículos cortos. El pico córneo es más ancho que alto y los rostrodontos están organizados en empalizada, son unicuspidados con el extremo liso y agudo. La cavidad bucofaríngea tiene dos pares de papilas infralabiales, cuatro papilas linguales, el pliegue mediano es triangular, los pliegues laterales son proyecciones simples, velo ventral y área glandular en la parte posterior. En el contenido intestinal se encontraron principalmente quistes y escamas de algas (Chrysophyta, Chrysophysea), frústulos de diatomeas e hifas de hongos.

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Cuidado parental y comportamiento de cardumen de larvas en *Leptodactylus insularum* (Anura, Leptodactylidae)

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Parental care of a similar nature has been noted in three species of *Leptodactylus* from two groups (*ocellatus* group: *L. ocellatus* and *L. insularum*; *melanonotus* group: *L. validus*). In these species, the female remains with the foam nest throughout development and then accompanies a school of tadpoles until metamorphosis. In addition, in *L. insularum*, tadpoles form densely packed schools of hundreds or thousands of individuals reminiscent of many *Bufo* species. In a two month study in Gamboa, Panamá, I examined whether parental care in *L. insularum* involved aggressive behavior and whether schooling behavior of tadpoles was stimulated by high densities and predators. Adult behavior was monitored daily nocturnally and diurnally, throughout the study. I performed two experiments with tadpoles. First, I tested whether tadpoles at different densities had different likelihood to form schools. Second, tadpoles were tested at two densities, with and without predators to see their schooling response. I found evidence of parental care, noting several schools of tadpoles with attendant adults. Furthermore, aggressive behavior by adults, including vocalizations, in the presence of tadpoles was noted on three occasions. In tadpoles the formation of schools was dependent on density. In addition insect predators acted as a stimulus to school formation in experiments at two tadpole densities.

Introducción

El término "cuidado parental" fue introducido por Trivers (1972), quien lo definió como "cualquier inversión por parte del progenitor en una prole determinada, que incrementa la oportunidad de supervivencia de la prole (y por lo tanto el éxito reproductivo) al costo de la capacidad del progenitor para invertir en otra prole". Desde entonces los patrones de comportamiento asociados a este término fueron definidos y analizados por numerosos autores quienes consideraron la relación entre fertilización externa e interna-cuidado por macho y/o hembra, y sus ventajas y desventajas para los padres y las crías (Smith, 1977,

WELLS, 1977; GROSS & SHINE, 1981; WITTENBERGER, 1981; SIMON, 1983; TOWNSEND et al., 1984; GROSS & SARGENT, 1985).

Existen pocos estudios sobre el cuidado parental en anfibios en comparación a aves y mamíferos. Este comportamiento se presenta en los tres órdenes de anfibios. Aunque solo fue reportado para el 6 % de las especies de anuros, se distribuye en diversas familias (CRUMP, 1996). CRUMP (1996) distingue seis modos de cuidado parental, de los cuales las especies del genero *Leptodactylus* representarían ejemplos de cuidado de huevos y cuidado de las larvas. Algunas funciones propuestas para el cuidado parental de huevos y larvas de anuros son: protección contra patógenos (especialmente hongos) y predadores, aireación de los huevos acuáticos; hidratación de los huevos terrestres; prevención de anormalidades en el desarrollo y de canibalismo (SIMON, 1983, CRUMP, 1996). Se postula que el beneficio del cuidado parental es incrementar la supervivencia de la prole. Entre los costos para el vigilante se considera el aumento de la vulnerabilidad a la predación, menor calidad y cantidad del alimento ingerido, y reducción de las oportunidades para aparearse (SIMON, 1983, TOWNSEND et al.,1984; CRUMP, 1996).

Una característica común de los miembros del genero *Leptodactylus* es la oviposición en una masa de espuma ya sea en la superficie del agua, o en cámaras incubatrices. Existen reportes de cuidado parental en especies del grupo *ocellatus* del genero *Leptodactylus* (HEYER, 1969): *L. chaquensis* (DE ALMEIDA PRADO et al., 2000), *L. ocellatus* (VAZ-FERREIRA & GEHRAU, 1975) y *L. insularum* (citada como *L. bolivianus* en WELLS & BARD, 1988). En los dos últimos casos el comportamiento de cuidado parental es similar. La hembra permanece junto al nido de espuma durante el desarrollo de los huevos y luego con el cardumen de larvas, día y noche hasta la metamorfosis. En *L. ocellatus*, VAZ-FERREIRA & GEHRAU (1975) registraron sonidos producidos por las larvas, que explicarían la posibilidad que tienen los renacuajos de detectar la presencia del grupo y orientarse hacia él, y podrían servir a la madre para guiarse hacia el cardumen aún estando a varios metros de distancia. Estos autores también registraron ataques de la madre y otros adultos a potenciales predadores en el área donde estaban los nidos o los renacuajos. WELLS & BARD (1988) determinaron en *L. insularum* un despliegue de movimientos que representaría una inusual y compleja forma de comunicación (física, química, o ambas) que permitiría a la hembra guiar a sus larvas. Movimientos de "bombeo" similares a los reportados para *L. insularum* (WELLS & BARD, 1988), tambien fueron observados en especies del grupo *melanonotus*: *L. validus* (DOWNIE, 1996), *L. leptodactyloides* (COCROFT & MORALES, comunicación personal) y en *L. podicipinus* (MARTINS, 1996). Otros miembros del genero con cuidado parental son *L. colombiensis* (ESTRADA, comunicación personal), *L. fallax* (LESCURE,1979, LESCURE & LETELLIER, 1983) y *L. fuscus* (LESCURE, 1973). En los dos últimos casos se determinó que la hembra permanece junto a la puesta de huevos. En este trabajo se estudió el comportamiento de cuidado parental en *L. insularum*, bajo la hipotesis de que el cuidado parental en esta especie implica un comportamiento agresivo ante posibles predadores.

La formación de cardúmenes (grupos relativamente estacionarios de cientos o miles de individuos), es una característica distintiva de ciertas larvas de anuros. Existen numerosas discusiones sobre si estos agrupamientos son equivalentes a los cardúmenes de peces. WASSERSUG et al. (1981) distinguen entre los cardúmenes de renacuajos y peces en que los primeros tienden a ser relativamente estacionarios y las distancias entre vecinos son azarosas. Algunos

autores, en un intento de definir y caracterizar los cardúmenes (de peces o larvas de anfibios), han distinguido entre distintos tipos de agrupamientos de acuerdo a sus características y al estímulo que los desencadenan (DUELLMAN & LESCURE, 1973; WASSERSUG, 1973; BEISWENGER, 1977; CALDWELL, 1989)

Además de los ya mencionados *L. insularum* y *L. ocellatus*, existen numerosos ejemplos de comportamiento de cardumen en larvas de anuros (WASSERSUG & HESSLER, 1971; BEISWENGER, 1975, 1977, 1981; WALDMAN, 1981; BREDEN et al., 1982; KEHR, 1994) BRANCH (1983) estudió la relación espacial, patrones de respiración y comportamiento de alimentación en cardúmenes de larvas de *Phyllomedusa vaillanti*; ALTIG & CHRISTENSEN (1981) estudiaron el comportamiento de cardúmenes de *Rana heckscheri*. CALDWELL (1989) describió tres modos de comportamiento de cardumen en larvas de *Hyla geographica*. Esta autora determinó que las larvas de *L. insularum* y *L. ocellatus* forman cardúmenes moderadamente polarizados en bordes sombreados de charcos o en el fondo de charcos, similar a los formados por las larvas de *Bufo* Se postula que la presencia de otras larvas estimula la formación de estas agregaciones en larvas de anuros (DUELLMAN & LESCURE, 1973; BEISWENGER, 1981) Algunos autores han hipotetizado sobre las posibles funciones de termoregulación y defensa de los cardúmenes (BREDER, 1967, O'HARA & BLAUSTEIN, 1981, CALDWELL, 1989; DE VITO et al., 1999) Como defensa, actuarían confundiendo al predador en la selección de una presa, especialmente cuando los predadores son insectos acuáticos (KEHR, 1994): de esta manera las agregaciones aumentarían la supervivencia de la puesta En este estudio se plantearon los objetivos de determinar si la formación de cardúmenes en *L. insularum* depende de la densidad larval ("estímulo social") y/o es estimulada por la presencia de predadores.

Existen distintas hipótesis sobre el mecanismo y función del cuidado parental en anfibios y sobre el comportamiento de cardumen. Las hipótesis planteadas en este trabajo son: (1) el cuidado parental en *L. insularum* implica un comportamiento agresivo ante posibles predadores; (2) la formación de cardúmenes de larvas en *L. insularum* depende de la densidad larval, (3) la presencia de predadores acuáticos es un estímulo para la formación de cardúmenes de larvas en *L. insularum* Para el estudio del comportamiento de cuidado parental se realizaron observaciones en el campo, y las hipótesis sobre cardumen de larvas se pusieron a prueba de manera experimental.

MATERIALES Y MÉTODOS

SISTEMA DE ESTUDIO

El área de estudio fue Kent's Marsh, ubicado en Gamboa, Panamá (9°7'30"N, 79°42'O), el cual es un charco temporario, de aproximadamente 430 × 45 m, cubierto con vegetación de tipo pastizal, la cual era cortada periódicamente. En la zona central del charco, donde se registró la mayor diversidad de anuros, había un mayor estancamiento de agua. Este charco fue seleccionado porque había mayor actividad de *L. insularum* que en otros cuerpos de agua del area *Leptodactylus insularum* es una especie de tamaño relativamente grande (largo hocico-cloaca medio hembra 86 16 mm, macho 85 6 mm), sin embargo difícil de localizar ya que esta crípticamente coloreada y se confunde con la vegetacion caida circundante

El estudio fue realizado durante la época lluviosa, desde fines de junio a mediados de septiembre de 1998.

En el área se determinaron cinco sectores de igual superficie, los cuales fueron monitoreados durante el día y la noche. El monitoreo se realizó simultáneamente mediante encuentros visuales (Crump & Scott, 1994), transectas acusticas (Zimmerman, 1994) y muestreo de transectas (Jaeger, 1994). Durante el día además de los métodos anteriores se realizó el reconocimiento de los sitios de puesta (Scott & Woodward, 1994). Los sitios donde estaban los nidos fueron marcados con cintas de color atadas a la vegetación circundante.

Cuidado parental

Cuando un adulto estuvo presente junto al nido o cardumen, se determinó la reacción del adulto cuando el investigador aproximaba la red de colectar larvas (considerado como hipotético predador) al nido o cardumen. Se consideraron tres tipos de reacciones: escape; agresión; no-agresión sin escape. La red fue colocada, en distintas ocasiones, junto al nido o cardumen, a 50 cm, a 1 m de distancia. Las observaciones se realizaron en el campo.

Comportamiento larval

¿La formación de cardúmenes depende de la densidad larval?

Para determinar si la formación de cardúmenes depende de la densidad larval, se colectó un cardumen de larvas del área de estudio. Este cardumen se dividió en grupos de 200, 100, 50 y 25 larvas que se colocaron en recipientes idénticos, de material plástico, de 35 cm de diámetro, en los que se colocaron 1,5 l de agua. Cuando se intentó colocar larvas a densidades más bajas (10 larvas por litro de agua) se observó una alta tasa de mortalidad, lo que obligó a interrumpir los experimentos reiteradas veces. Para descartar la posibilidad de que la calidad del agua fuera responsable de la mortandad se colocaron las larvas en agua de lluvia y después en agua corriente estacionada en recipientes un tiempo suficiente para que se evapore el cloro que pudiera tener, en ambos casos las larvas murieron. Finalmente, para los experimentos se opto por utilizar agua del charco donde eran colectadas las larvas diluida con agua corriente estacionada y no realizar tratamientos a tan bajas densidades.

Los experimentos se realizaron en laboratorio, y consistieron en determinar si había formación de cardumen en los diferentes tratamientos. Se consideró como cardumen a los agrupamientos de larvas (larvas contiguas unas a otras) y a estos se los considero en cinco categorías: (0) 0 % de larvas agrupadas, (1) hasta 10 %, (2) hasta 25 %; (3) hasta 50 %, (4) hasta 100 %. Durante una hora se registro cada 10 minutos presencia/ausencia y categoria de agrupamiento en el instante en que se observaban los recipientes, y después una vez cada hora por 8 horas más.

Los datos se analizaron con el test de Kruskal-Wallis, ya que no estaban distribuidos normalmente y no presentaban varianzas homogeneas. Se realizó a posteriori un test de Dunn para determinar entre que pares de tratamientos había o no diferencias significativas.

¿La formación de cardumen es estimulada por la presencia de predador acuático?

Para responder este punto se realizaron pruebas de palatabilidad a fin de seleccionar un buen predador de larvas de anfibios. Estos experimentos consistieron en colocar a los renacuajos en recipientes con potenciales predadores (coleópteros acuáticos y larvas acuáticas de insectos) y seleccionar a los predadores que atacaban más rápido y comían más rápidamente a las larvas de anuros. Los mejores predadores fueron larvas de Hydrophylidae (Coleoptera) (longitud media: 27,36 mm), que eran comunes en el charco donde estaban los renacuajos. Estas larvas atacaban rápidamente y sostenían con su aparato bucal al renacuajo mientras lo ingerían en corto tiempo. Los tratamientos consistieron en recipientes idénticos, con igual densidad de larvas de un mismo cardumen, con predador (una larva de Hydrophylidae en cada tratamiento) y sin predador. Cada cinco minutos, durante dos horas, se determinó si había formación de cardumen en cada tratamiento. Las categorías de agrupamientos consideradas fueron. (0) sin agrupamiento; (1) ≤ 5 larvas; (2) ≤ 20 larvas; (3) ≤ 50 larvas; (4) ≤ 100 larvas, (5) < 200 larvas; (6) < 300 larvas. No hubo reposición de los renacuajos ingeridos por el predador, ya que en el tiempo que duraron los experimentos, esta predación no hizo variar considerablemente la cantidad de renacuajos.

Se realizaron dos experimentos independientes. En uno de ellos fueron colocadas 300 larvas por recipiente, y se hicieron tres réplicas por tratamiento (con predador y sin predador). Estas larvas pertenecían a un cardumen que había eclosionado cinco días antes, y en el que se contabilizaron 2014 larvas. En el otro experimento se colocaron 100 larvas por recipiente, se realizaron dos réplicas por tratamiento (con predador y sin predador). En este cardumen se contabilizaron 481 larvas, en estadios 29-37 de la tabla de GOSNER (1960). Como control se empleó larvas de *Physalaemus pustulosus*, de estadios 29-31 de la tabla de GOSNER (1960), cuyos nidos fueron colectados en la misma zona que los de *L. insularum*. El control fue empleado para comparar el comportamiento de los renacuajos cuando forman cardumen de cuando no lo hacen, ya que las larvas de *P. pustulosus* colocadas a la misma densidad, y en presencia de los mismos predadores nadaban independientemente, sin colocarse contiguas unas de otras o demostrar algún tipo de agrupamiento.

Los datos se analizaron con un test de independencia (chi cuadrado) entre grupos (con depredador / sin depredador) y respuestas (con agrupación / sin agrupación).

RESULTADOS

De los 31 días que estuvo presente *L. insularum*, 25 estuvieron en la zona central del área de estudio, la cual, a diferencia de las otras zonas, tuvo agua estancada durante todo el período de estudio. En ella se registró la mayor cantidad de especies de anuros (hasta 12 especies), y presentaba mayor heterogeneidad, en cuanto a la fisonomía de la vegetación, que el resto del área. Los nidos y cardúmenes también se encontraron en esta zona. Se registraron un total de 8 nidos y 7 cardúmenes. Los nidos observados tenían forma de corona con un orificio en el centro. Los nidos, al igual que los adultos, estaban generalmente en áreas con vegetación alta (vegetación de altura menor o igual a 1,6 m), tipo pastizal. Fue muy común encontrar los nidos sucesivos en los mismos sitios en donde habían otros anteriormente

Cuidado parental

Junto a algunos cardúmenes había adultos, los cuales huían ante la presencia del investigador ($n = 2$) o demostraban un comportamiento agresivo ($n = 3$). El comportamiento agresivo fue registrado en tres ocasiones, el 30 de Julio, el 12 y el 25 de Agosto de 1998. No se pudo determinar el sexo de estos adultos, o si se trataba del mismo o diferentes individuos. El comportamiento agresivo fue observado en dos ocasiones durante el día y en una durante la noche. En los tres casos este despliegue consistía en que cuando se simulaba colectar larvas con una red (colocando la red sobre las larvas), el adulto saltaba instantáneamente sobre la red, mordiendo, y en algunos casos emitiendo un grito o gruñido El adulto luego saltaba lejos de ella (menos de 1 m), quedando de espaldas al cardumen y a la red. Al colocar de nuevo la red en contacto con el agua en la zona donde estaban las larvas, se volteaba y volvía a saltar sobre la red. No era necesario mover la red o agitar con ella el agua para que el adulto reaccionara atacando inmediatamente. Este comportamiento se repitió sucesivamente hasta por dos horas en cada adulto ($n = 20$ a 25 en cada una de las tres ocasiones)

En dos de las tres ocasiones en que se registró el comportamiento agresivo, se colocó luego la red a una mayor distancia (aproximadamente a 1 m de un individuo en una ocasión y a 50 cm en otra ocasión). En estos casos el ataque no fue instantáneo, tardando de 20 a 40 segundos, pero hubo agresión en el 70 % de las veces en que se colocó la red a 50 cm ($n = 20$), y en el 66.6 % cuando se la colocó a 1 m ($n = 15$). Cuando la red fue colocada a aproximadamente 1 m, el adulto no la alcanzó de un solo salto, se acercó y cuando estuvo a la mitad de la distancia, saltó sobre ella. En esta misma ocasión se colocó la red a poca distancia del adulto (menos de 50 cm), pero en una zona sin larvas y, aunque demoró más, reaccionó saltando sobre la red y volviendo a la zona donde estaban las larvas en el 100 % de los casos ($n = 15$) Cuando se le colocó la red a mayor distancia (a 1 m aproximadamente), en una zona sin larvas, el adulto no reaccionó.

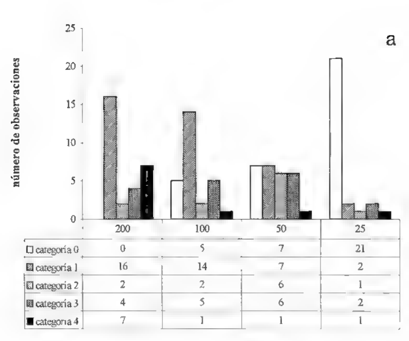
Comportamiento larval

¿La formación de cardúmenes depende de la densidad larval?

Los resultados demuestran que a bajas densidades no hay tendencia a la formación de cardumen ($H = 23{,}018$; $P < 0{,}0001$). La tendencia a formar cardumen mostró una diferencia altamente significativa ($P < 0,0001$) entre los tratamientos de 200 y 25 larvas; y una diferencia significativa ($P < 0,05$) entre las densidades de 100 y 25 larvas y las densidades de 50 y 25 larvas, mientras que no hubo diferencias significativas ($P > 0,05$) en la tendencia a formar cardumen entre los grupos de 200 y 100 larvas, 200 y 50 larvas, y 100 y 50 larvas. Por lo tanto los resultados demuestran que el grupo de 25 larvas por tratamiento es el que no demuestra una significativa tendencia a formar cardúmenes (fig. 1).

¿La formación de cardumen es estimulada por la presencia del predador acuático?

En experimentos de predacion realizados con 300 larvas por tratamiento, la tendencia a formar cardumen fue mayor en presencia del predador que en ausencia del mismo (χ^2 =



	200	100	50	25
categoría 0	0	5	7	21
categoría 1	16	14	7	2
categoría 2	2	2	6	1
categoría 3	4	5	6	2
categoría 4	7	1	1	1

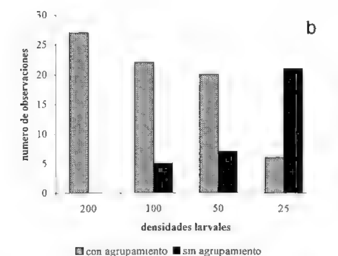
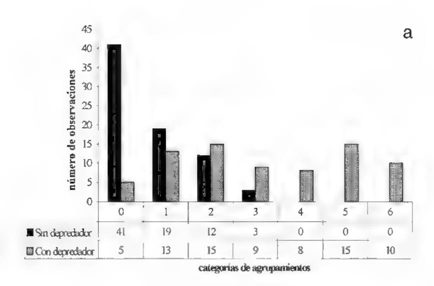
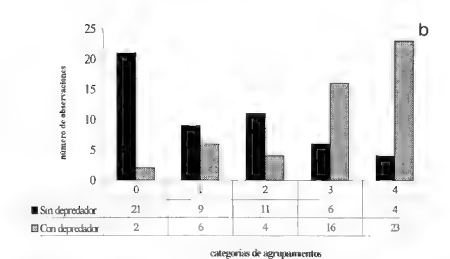


Fig 1 (a) Categorías de agrupamientos a diferentes densidades larvales en *Leptodactylus insularum* Categorías consideradas (0) 0 % de larvas agrupadas, (1) hasta 10 %, (2) hasta 25 %, (3) hasta 50 %, (4) hasta 100 % (b) Tendencia a formar cardúmenes a diferentes densidades, considerando únicamente la presencia (categoría de agrupamiento 1 a 4) o la ausencia (categoría de agrupamiento 0) de agrupamiento



	0	1	2	3	4	5	6
Sin depredador	41	19	12	3	0	0	0
Con depredador	5	13	15	9	8	15	10



	0	1	2	3	4
Sin depredador	21	9	11	6	4
Con depredador	2	6	4	16	23

Fig. 2. – (a) Número de observaciones de agrupamientos de larvas por categorías, utilizando 300 larvas por tratamiento. (b) Número de observaciones de agrupamientos de larvas por categorías empleando 100 larvas por tratamiento. Categorías consideradas: (0) sin agrupamiento, (1) ≤ 5 larvas, (2) ≤ 20 larvas, (3) ≤ 50 larvas, (4) ≤ 100 larvas, (5) ≤ 200 larvas; (6) ≤ 300 larvas.

221.92; *df* = 1; $P < 0.001$) (fig 2A). Lo mismo ocurrió en los experimentos realizados con 100 larvas por tratamiento ($\chi^2 = 188.02$; *df* =1; $P < 0.001$) (fig 2B).

DISCUSIÓN

CUIDADO PARENTAL

El cuidado parental en *L. insularum* ha sido reportado por WELLS & BARD (1988) en la misma área en la que fue hecho este estudio (Gamboa, Panamá) Se pudo corroborar dicho comportamiento aunque en algunos casos las larvas no se encontraban en compañía de un adulto, posiblemente porque el descubrimiento de los nidos y los cardúmenes implicaba disturbio de la vegetación circundante, y podría causar que los adultos escaparan. Estos autores determinaron un despliegue de movimientos, por el cual el adulto se comunicaría con las larvas y las guiaría a sectores del cuerpo de agua con suficiente profundidad para completar el desarrollo. Este despliegue consiste en "bombeos" en el agua que comienzan cuando la hembra arquea su espalda y eleva sus patas posteriores y cloaca sobre la superficie del agua, luego su parte posterior desciende hasta el agua produciendo ondas en la superficie que se dirigen hasta los renacuajos. DOWNIE (1996) observó "movimientos de bombeo" similares en *L. validus*, aunque sus datos no demuestran que estos movimientos tengan la función de guiar a las larvas, posiblemente porque sus observaciones fueron hechas durante el día, y *L. insularum* fue observado guiando a las larvas principalmente durante la noche (WELLS & BARD, 1988) En este estudio no se observó este despliegue, ni tampoco el desplazamiento de las larvas en dirección a la madre, como lo describen estos autores. La observación de que es la hembra quien realiza el cuidado estaría contradiciendo las hipótesis de "la certeza paterna" y la del "orden de liberación de los gametos" (GROSS & SHINE, 1981). La primera hipótesis propone que es más probable que las familias con fertilización externa presenten cuidado paternal, porque la certeza de paternidad es mayor que en los casos con fertilización interna. La segunda hipótesis propone que el cuidado parental es el resultado de la diferente oportunidad para abandonar a los cigotos, de manera que el sexo que desova último, debería realizar el cuidado.

Los nidos que se encontraron estuvieron siempre en los mismos sitios, esto podría ser un indicio de fidelidad al sitio. SEXTON (1962) reportó comportamiento de territorialidad en esta especie, él observó que los machos cantan desde depresiones localizadas en el centro del nido y los defienden de la invasión de otros machos. Las observaciones de WELLS & BARD (1988) y VAIRA (1997) (quienes determinaron que las hembras realizan el cuidado parental) se contradicen con las hechas previamente por SEXTON (1962). Tal vez el macho y la hembra realizan el cuidado de la puesta. A este tipo de cuidado se le da el nombre de "anfisexual", y ha sido reportado para *Cophixalus parkeri* (SIMON, 1983), para algunos leptodactylidos, dendrobatidos y myobatrachidos (MCDIARMID, 1978). En este estudio no se pudo comprobar si era el macho o la hembra el que realizaba el cuidado, ya que no se quisieron colectar los individuos, para observar el comportamiento agresivo sin causar demasiado disturbio. Serían necesarias observaciones que clarifiquen cual de los tres tipos de cuidado parental se presenta efectivamente en esta especie.

De acuerdo a los resultados obtenidos, el cuidado parental en *L. insularum* implica comportamiento agresivo. El ataque de los adultos hacia un hipotético predador soporta la hipótesis de que el comportamiento epimelético en esta especie tendría funcion de defensa del cardumen de larvas contra predadores. Esta misma función fue determinada en *L. ocellatus* (Vaz-Ferreira & Gehrau, 1975). En esta especie la hembra cuida al nido ubicándose en el orificio central del mismo. Aunque los nidos de *L. insularum* observados presentaban un orificio en el centro, nunca se vieron adultos instalados en él. Cuando los adultos estuvieron con el cardumen, lo hicieron desde algún sustrato próximo, como vegetación caída. Wells & Bard (1988) observaron a una hembra de *L. insularum* ubicada en el centro del grupo de renacuajos. A diferencia de *L. insularum*, en donde la hembra conduce a las larvas, en *L. ocellatus*, aparentemente la hembra sigue a los renacuajos (Vaz-Ferreira & Gehrau, 1975).

Durante su vigilia, las hembras de *L. ocellatus* huyen al acercarse "una persona, dedos o un pájaro", o atacan saltando desde el orificio y mordiendo. Durante el salto emiten a veces un grito de alarma (Vaz-Ferreira & Gehrau, 1975). De manera similar, el grito emitido por *L. insularum* cuando saltaba sobre la red de colectar larvas, tendría función agresiva contra el predador de renacuajos. Wells & Bard (1988) no observaron ataques agresivos en *L. insularum*. Vaira (1997) reportó ataques agresivos similares en hembras de *L. insularum* (como *L. bolivianus*). Las hembras atacaban un palo colocado sobre sus cabezas, y luego una bola de plástico atada a un palo a 20 cm de ellas, aunque no aclara si fueron colocadas en las proximidades del cardumen. En el presente estudio los adultos se encontraron ocultos bajo la vegetación durante el día, al igual que las hembras observadas por Vaira (1997). Sin embargo este autor registró ataques sólo durante la noche, y en este estudio se registraron durante el día en dos de las tres ocasiones en que fue observado. Las hembras de *L. ocellatus* en Uruguay (Vaz- Ferreira & Gehrau, 1975) y Córdoba (Vaira, 1997) también atacaron durante el día. Ataques similares también fueron registrados en el Ranidae africano *Pyxicephalus adspersus*, en esta especie el macho acompaña al cardumen y ataca inclusive a grandes vertebrados (Balinsky & Balinsky, 1954; Rose, 1956; Poynton, 1957). Además de las especies de *Leptodactylus* anteriormente mencionadas, *L. ocellatus*, *L. validus* y *L. insularum*, también existen reportes de cuidado parental en *L. chaquensis* (De Almeida Prado & Uetanabaro, 2000), *L. podicipinus* (Martins, 1996), *L. colombiensis* (Estrada, comunicación personal), *L. fallax* y *L. fuscus* (Lescure, 1973, 1979, 1983). Dada la falta de información sobre la ocurrencia del cuidado parental en otras especies de *Leptodactylus* y sobre las relaciones filogenéticas del género, por el momento no es posible establecer si el cuidado parental es una sinapomorfía solamente de algunas especies del género, de todo el género o de un clado más inclusivo. En un análisis filogenético, el cuidado parental podría ser considerado como más de un carácter según lo realice el macho, la hembra o ambos; implique o no comportamiento agresivo hacia predadores; abarque el período de huevos y larvas, sólo el de huevos o sólo el larvario.

Comportamiento larval

Efecto de la densidad larval en la formación de cardumen

Los resultados obtenidos indican que a baja densidad, los renacuajos no tienden a formar cardumen. Se postula que el "estímulo social", es decir el estímulo generado por la

presencia de otras larvas, es una de las causantes de las agregaciones de larvas de anuros (DUELLMAN & LESCURE, 1973; BEISWENGER, 1981). Posiblemente, como a bajas densidades la probabilidad de encuentro entre larvas es menor, no actúe el estímulo social y por lo tanto no haya formación de cardumen. Por otro lado la mortalidad observada cuando se colocaron larvas a muy bajas densidades (10 larvas por litro de agua), plantea el interrogante de si la causa de la misma pudiera ser precisamente la baja densidad larval.

Efecto de la predación en la formación de cardumen

Los resultados de los experimentos de laboratorio demuestran que la presencia de predadores estimula la formación de cardúmenes de larvas en *L. insularum*. En larvas de *Hyla regilla* también se determinó un nivel más alto de agregación en presencia de víboras que actuaban como predadores (DE VITO et al., 1999). El hábito de formar agregaciones confiere ventajas tanto a predadores como a presas (MAJOR, 1978). En las presas, incrementa su habilidad para escapar al ataque del predador, y en este último aumenta el exito de captura. De acuerdo con MAJOR (1978), los predadores se orientan hacia las presas mediante el estímulo visual. Durante el tiempo que requiere esta orientación, el predador recibe la información necesaria para predecir cuando y donde abrir la boca para un ataque seguro. Este patrón de acción fija puede ser crítico, limitando la maniobrabilidad del predador durante los milisegundos finales del ataque. Así el predador podría no ser confundido por un cardumen de presas, pero pierde el tiempo necesario para alinearse con una presa individual para un ataque exitoso. Es en este contexto donde el comportamiento de formar cardúmenes tiene valor para la supervivencia de las presas. En el caso de larvas de anuros, KEHR (1994) determinó que aunque los cardúmenes de larvas pueden producir "confusión" del predador en la selección de una presa, esta interacción se produciría especialmente cuando los predadores son ciertos insectos acuáticos, como fue el caso de los experimentos realizados en este estudio.

Otros factores, además de la presencia de predadores y del estímulo "social", han sido propuestos para explicar las funciones y las causas de la formación de cardúmenes: estímulos "ambientales", como luz, temperatura, alimento, actuarían estimulando la formación de cardúmenes (WASSERSUG & HESSLER, 1971; DUELLMAN & LESCURE, 1973; BEISWENGER, 1975, 1977, 1981; KATZ et al., 1981; O'HARA & BLAUSTEIN, 1981; CALDWELL, 1989).

CONCLUSIONES

Las ventajas y los costos del cuidado parental son múltiples, probablemente dependerán no sólo de la especie que lo presente, sino del ambiente con el que se enfrenten los individuos o poblaciones individuales. Del mismo modo ocurrirá con las agregaciones de larvas de anuros. En base a los datos obtenidos en este estudio se puede concluir que en *L. insularum* el cuidado parental implica un comportamiento agresivo y tendría una función de defensa contra predadores, esto no descarta otras posibles funciones a ser evaluadas. Los experimentos realizados demuestran que la formación de cardumenes responde al estímulo social (la presencia de otras larvas, a densidades suficientemente altas) y a la presencia de predadores.

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On the relevance of the character "absence of epicoracoid horns" in the systematics of anurans

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Several authors consider the character "absence of epicoracoid horns" a synapomorphy of the group that includes the anuran families Dendrobatidae, Hyperoliidae, Microhylidae, Ranidae and Rhacophoridae (i.e., Ranoidea). However, others have suggested that this condition is plesiomorphic (i.e., epicoracoid horns are absent in several non-Ranoidea frogs) and that Ranoidea frogs possess epicoracoid horns. The pectoral girdles of several Ranoidea and non-Ranoidea frogs were sectioned histologically, and all had epicoracoid horns. The presence of epicoracoid horns in Ranoidea frogs suggests the character "absence of epicoracoid horns" is not a synapomorphy of this group.

INTRODUCTION

Several authors (GRIFFITHS, 1963, KLUGE & FARRIS, 1969; LYNCH, 1973; DUELLMAN & TRUEB, 1985) hypothesized that the families Dendrobatidae, Hyperoliidae, Microhylidae, Ranidae and Rhacophoridae form a monophyletic group supported by the synapomorphy "absence of epicoracoid horns" (i.e., posteriorly directed processes of the epicoracoid cartilages. GRIFFITHS, 1957, 1960*a-b*, 1963)

The hypothesis that the character "absence of epicoracoid horns" is a synapomorphy of Ranoidea is questionable, first, because the absence of epicoracoid horns (MCDIARMID, 1971, TRUEB, 1973, RUIZ-CARRANZA & HERNANDEZ-CAMACHO, 1976, GRANDISON, 1981, LYNCH & RUIZ-CARRANZA, 1982, MYERS & FORD, 1986, TYSON, 1987) in several non-Ranoidea frogs (i.e., *Atelopus*, *Atopophrynus*, *Brachycephalus*, *Dendrophryniscus*, *Didynamipus sjoestedti*, *Melanophryniscus*, *Oreophrynella*, *Osornophryne*, *Rhinophrynus dorsalis*) suggests this character is plesiomorphic at the level of Ranoidea, and second, because it has been suggested (KAPLAN, 1994) that Ranoidea frogs have epicoracoid horns that are fused, indistinguishably, to the sternum. However, the absence of epicoracoid horns in non-Ranoidea frogs and their

presence in Ranoidea frogs is controversial (KAPLAN, 1994; TYSON, 1987) and requires confirmation through detailed (i.e., histological) morphological examinations.

Herein, the girdles of several species of Ranoidea and non-Ranoidea frogs are examined through histological sectioning in order to assess the distribution of the character "absence of epicoracoid horns" in frogs. The hypothesis that the character "absence of epicoracoid horns" is a synapomorphy of Ranoidea is evaluated in light of the new morphological observations.

MATERIALS AND METHODS

The medial portion of the ventral elements (omosternum, clavicles, procoracoids, epicoracoids, coracoids, sternum) of the pectoral girdle of individuals at different developmental stages (GOSNER, 1960, in parentheses) of the following species was sectioned (App. 1). Ranidae: *Rana blairi* (44, adult); Dendrobatidae: *Colostethus subpunctatus* (44, 46, adult); Microhylidae: *Gastrophryne carolinensis* (43, 44, adult), Hyperoliidae, *Kassina senegalensis* (44, adult), Rhacophoridae: *Rhacophorus moltrechti* (44, adult); Bufonidae *Oreophrynella quelchii* (adult), *Melanophryniscus stelzneri* (adult) and *Dendrophryniscus brevipollicatus* (adult); and Brachycephalidae, *Brachycephalus ephippium* (adult). Abbreviations for institutions are as follow: ICN, Instituto de Ciencias Naturales, Universidad Nacional de Colombia; UMMZ, University of Michigan Museum of Zoology.

The medial portion of the ventral elements of the pectoral girdles of adults and juveniles was excised by cutting through the right and left procoracoid cartilages, clavicles, coracoid bones, and around the omosternum and sternum, when present, the medial portion of the ventral elements of the pectoral girdles was removed, decalcified (Cal-Ex II, Fisher Scientific), and sectioned transversely from the anterior tip of the omosternum to the posterior tip of the sternum, *Brachycephalus ephippium* was sectioned from the tip of the snout to the posterior part of the girdle. Tissues were embedded in paraffin (WESSNER, 1960), sectioned (15 μm), and stained with hematoxylin eosin. Histological and osteological terminologies follow those of FAWCETT (1986) and DE VILLIERS (1924), respectively.

Herein, I consider the epicoracoid horns to be parts of the epicoracoid cartilages that extend posteriorly to the posteromedial part of the coracoid

RESULTS

Descriptions of the zonosternal articulation (fig 1) of non Ranoidea and Ranoidea frogs.

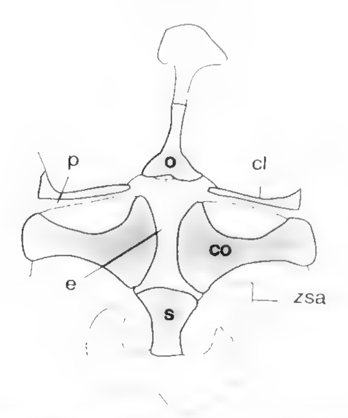


Fig. 1. – Ventral view of the pectoral girdle of *Rana blairi*, showing the interaction between the right and left halves as the meet medially. cl, clavicle; co, coracoid; e, epicoracoid; o, omosternum; p, procoracoid; s, sternum; zsa, zonosternal articulation. Grey, bone; clear, cartilage.

Non-Ranoidea frogs

In *Dendrophryniscus brevipollicatus*, *Melanophryniscus stelzneri* and *Oreophrynella quelchii*, each epicoracoid cartilage bears a tapered, divergent cartilaginous process that extends posteriorly from the coracoids (fig. 4A-C). In *Brachycephalus ephippium*, the posterior processes of the epicoracoids are short, thin, not diverging from, and firmly attached (but not indistinguishably fused) to, each other (fig. 4D).

In *Oreophrynella quelchii*, the *m. sternoepicoracoideus* does not insert on the posterior terminus of the posterior processes of the epicoracoids. In *Melanophryniscus stelzneri*, a laterally directed ligament inserts on the posterior terminus of each process, the *m. sternoepicoracoideus* does not insert on the ligaments. In *Dendrophryniscus brevipollicatus*, a posteriorly directed ligament inserts on the posterior terminus of each process, these ligaments are long and extend parallel to the lateral margins of the sternum, the *m. sternoepicoracoideus* inserts on the posterior ends of these ligaments. In *Brachycephalus ephippium* two short, wide

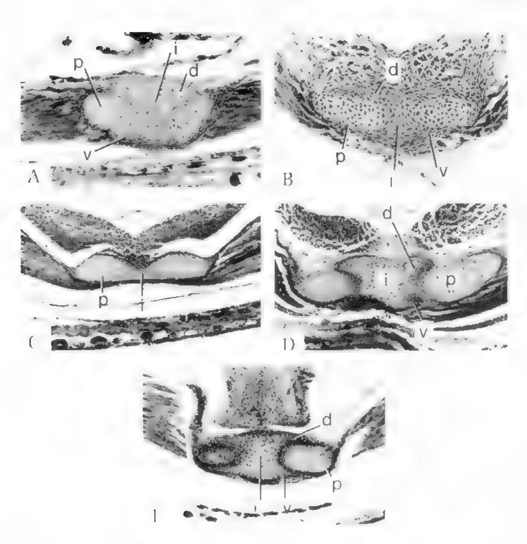


Fig. 2. – Transverse sections of the zonosternal articulation of the premetamorphic individuals (developmental stage in parenthesis) of the following species (A) *Colostethus subpunctatus* (46), (B) *Gastrophryne carolinensis* (43), (C) *Kassina senegalensis* (44), (D) *Rana blairi* (44), (E) *Rhacophorus moltrechti* (44) d, dorsal sternal blade, i, sternal isthmus, p, posterior process of the epicoracoids, v ventral sternal blade

slips of the *m. sternoepicoracoideus* insert on the posterior termini of the posterior processes of the epicoracoids; no ligament mediates the insertion of the *m. sternoepicoracoideus* on the posterior processes of the epicoracoids.

As seen in sectional view, in *Dendrophryniscus brevipollicatus*, *Melanophryniscus stelzneri* and *Oreophrynella quelchii*, each lateral margin of the isthmus of the sternum bears a lateral

groove formed by dorsal and ventral blades (fig. 4A-C). In *Brachycephalus ephippium*, the sternum is absent.

In *Dendrophryniscus brevipollicatus*, *Melanophryniscus stelzneri* and *Oreophrynella quelchii*, the posterior processes of the epicoracoids are housed in the sternal grooves (fig. 4A-C). In *D. brevipollicatus*, *M. stelzneri* and *O. quelchii*, the anterior portion of the posterior processes of the epicoracoids has its dorsal, medial and ventral surfaces separated from the sternum by a gap. In *D. brevipollicatus* and *M. stelzneri*, a thick ligament surrounds and attaches the lateral surfaces of the posterior processes of the epicoracoids to the dorsal and ventral sternal blades; posteriorly, the posterior processes of the epicoracoids run parallel to the lateral margins of the sternum for a short distance; in *M. stelzneri*, the posterior ends of the processes are firmly attached to the sternum by ligaments. In *O. quelchii*, the posterior parts of the posterior processes of the epicoracoids are fused to the sternum.

Ranoidea frogs

In premetamorphic individuals of *Colostethus subpunctatus*, *Gastrophryne carolinensis*, *Kassina senegalensis*, *Rana blairi* and *Rhacophorus moltrechti*, each epicoracoid cartilage bears a blunt, tapered, ovoid (in transverse section), divergent cartilaginous process that extends posteriorly from the coracoids (fig. 2A-E); the *m. sternoepicoracoideus* (i.e., epicoracoid horn muscle: Griffiths, 1963) does not insert on the posterior terminus of the process. As seen in sectional view, each lateral margin of the isthmus of the sternum bears a lateral groove formed by dorsal and ventral blades; the posterior processes of the epicoracoids are housed in the sternal grooves and fused to the sternum.

In adult individuals of *Colostethus subpunctatus*, *Rana blairi*, and *Rhacophorus moltrechti*, the medial surfaces of the posterior processes of the epicoracoids are separated from the sternum by a gap (fig. 3A-C). In *R. blairi* and *R. moltrechti*, the posterior tips of the posterior processes of the epicoracoids are mostly eroded; thus, the posterior parts of the sternal grooves are empty or contain few fragments of the processes. In *R. moltrechti*, the sternal isthmus is thinner (in transverse section) than the posterior processes of the epicoracoids. In *Gastrophryne carolinensis* and *Kassina senegalensis*, the posterior processes of the epicoracoids are indistinguishably fused to the sternum. The ventral sternal blade is absent in *Colostethus subpunctatus*.

Discussion

All the species of frogs examined exhibit two processes of the epicoracoids that extend posteriorly to the coracoids. In all Ranoidea frogs examined, the posterior processes of the epicoracoids are evident in premetamorphic stages, however, these processes in adults can be partly eroded (e.g., *Rana blairi*, *Rhacophorus moltrechti*) or indistinguishably fused to the sternum (e.g., *Gastrophryne carolinensis* and *Kassina senegalensis*). In all non-Ranoidea frogs examined (i.e., *Brachycephalus ephippium*, *Dendrophryniscus brevipollicatus*, *Melanophrynis-*

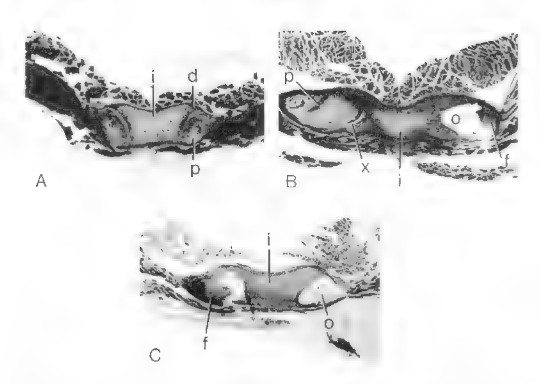


Fig. 3. Transverse sections of the zonosternal articulation of adult individuals of the following species (A) *Colostethus subpunctatus*; (B) *Rana blairi*; (C) *Rhacophorus moltrechti* d, dorsal sternal blade, i, sternal isthmus, f, fragment of one of the posterior processes of the epicoracoids, o, empty sternal groove; p, posterior process of the epicoracoid; x, gap.

cus stelzneri, *Oreophrynella quelchii*), the posterior processes of the epicoracoids are evident in adults.

The posterior processes of the epicoracoids of all the species here studied must be considered epicoracoid horns because, like the horns of arciferal frogs (e.g., *Ascaphus*, *Bufo*. GRIFFITHS, 1963), they are posterior extensions of the epicoracoid cartilages and show the same topographic relation to other body parts (e.g., they are housed in sternal grooves).

This study challenges previous reports (MCDIARMID, 1971; TRUEB, 1973, TYSON, 1987) that epicoracoid horns are absent in *Brachycephalus*, *Dendrophryniscus*, *Melanophryniscus* and *Oreophrynella*. The presence of epicoracoid horns in these taxa suggests that all non-Ranoidea frogs have epicoracoid horns (however, note that the presence of epicoracoid horns in taxa such as *Osornophryne*, *Geobatrachus*, *Atopophrynus*, *Didynamipus* and *Rhinophrynus dorsalis* still needs to be demonstrated), and therefore, that the character "absence of epicoracoid horns" is not pleisiomorphic at the level of Ranoidea However, the character "absence of epicoracoid horns" is invalid as a synapomorphy of Ranoidea because, as this study suggests, all Ranoidea frogs have epicoracoid horns (note that the monophyly of

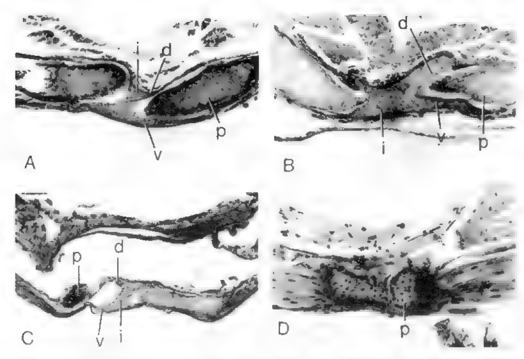


Fig. 4. - Transverse sections of the zonosternal articulation of adult individuals of the following species. (A) *Dendrophryniscus brevipollicatus*, (B) *Melanophryniscus stelzneri*, (C) *Oreophrynella quelchii*, (D) *Brachycephalus ephippium*. d, dorsal sternal blade; i, sternal isthmus, p, posterior process of the epicoracoid, v, ventral sternal blade.

Ranoidea is still supported by the characters "epicoracoid cartilages completely fused" and "medial end of the coracoids wider than lateral end": Ford & Cannatella, 1993).

I found considerable morphological variation in the epicoracoid horns of frogs: these can be fused or free from the sternum, short or long, rounded or thread-like, extending parallel to the lateral edge of the sternum or not. The systematic value of these characters, and the independence from each other, is currently unknown.

Resumen

Varios autores consideran que el caracter "ausencia de cuernos epicoracoidales" es una sinapomorfia del grupo (Ranoidea) que incluye a las familias Dendrobatidae, Hyperoliidae, Microhylidae, Ranidae y Rhacophoridae. Sin embargo, se ha sugerido que esta condición es plesiomorfica (esta presente en varios anuros que no son Ranoidea) y que los anuros Ranoidea tienen cuernos epicoracoidales. Las cinturas pectorales de varios anuros Ranoidea y no Ranoidea fueron seccionados histologicamente y se encontro que todos tienen cuernos

epicoracoidales. La presencia de cuernos epicoracoidales en anuros Ranoidea sugiere que el caracter "ausencia de cuernos epicoracoidales" no es una sinapomorfia de este grupo.

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APPENDIX I
SPECIMENS EXAMINED

Rana blairi (UMMZ 224284-5); *Colostethus subpunctatus* (ICN 15822, 23308; UMMZ 224288); *Gastrophryne carolinensis* (UMMZ 108418, 224286-7); *Rhacophorus moltrechti* (UMMZ 199779, 201298); *Kassina senegalensis* (UMMZ 151702, 210193); *Oreophrynella quelchii* (UMMZ 85141); *Melanophryniscus stelzneri* (UMMZ 166804); *Brachycephalus ephippium* (UMMZ 103568); *Dendrophryniscus brevipollicatus* (UMMZ 204307).

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BOURRET, R., 1942. – *Les batraciens de l'Indochine*. Hanoi, Institut Océanographique de l'Indochine: i-x + 1-547, pl. 1-4.

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